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Interhemispheric EEG Coherence during Sleep and Wakefulness in Left- and Right-Handed Subjects

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REM sleep is associated with the production of complex imagery sequences. Yet research is divided as to whether different brain regions are more or less coordinated in their functioning at this time. Some research suggests that there may occur a functional disconnection of the left and right cerebral hemispheres during REM sleep which is similar to the disconnection syndrome seen after corpus callosotomy. Other research suggests that an increase in interhemispheric coordination occurs. On the assumption that hemispheric coordination is reflected in the EEG coherence measure, we explored differences in interhemispheric coherence recorded in six left- and six right-handed normal subjects during periods of wakefulness, stage REM, stage 2, and stage 3/4 sleep. Strong evidence was found that mean EEG coherence values are larger during sleep than during waking and that they are approximately equal for the different stages of sleep. Frontal electrode placements demonstrated a slightly different pattern of coherence than central, parietal, or occipital placements. Furthermore, coherence values were larger for left-handed subjects over the occipital region during wakefulness, stage 2, and stage REM sleep, but not during stage 3/4 sleep. Coherence was not different for male and female subjects. These findings oppose the interpretation that a functional disconnection of hemispheres occurs during REM sleep and favor the interpretation that sleep in general is a state of heightened cortical coordination. Moreover, greater interhemispheric coherence over occipital brain regions in left-handed subjects suggests possible differences in the cognitive processes of these subjects during waking and dreaming states.

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INTRODUCTION

Functional hemispheric disconnection in REM sleep. One of the earliest significant discoveries about REM sleep was its regular association with dream imagery (e.g., Dement & Kleitman, 1957). This association suggested that neural activity of the brain—and in particular of the left and right hemispheres of the brain—might be as active and coordinated during REM sleep as during wakefulness. Yet the available research is still inconclusive on this point.

Two perspectives on hemispheric connection are frequently cited in the literature; these differ on the role they ascribe to the interhemispheric transfer of information during REM sleep. On the one hand, what may be referred to as the *functional disconnection* perspective suggests that information transfer is diminished during REM sleep. One component of this point of view is that the similarities between dream mentation and mentation associated with right hemisphere activity in waking states suggest that dream production might result primarily from right hemisphere activity (Bakan, 1978; Broughton, 1975; Galin, 1974). Several early studies of human subjects with right-sided lesions support this possibility (Cathala, Laffont, Gilbert, Esnault, Siksou, & Ming, 1982; Epstein, 1979; Humphrey & Zangwill, 1951; Kerr & Foulkes, 1981), and some neurophysiological studies also show a greater activation of the right hemisphere during REM sleep (Goldstein, Stoltzfus, & Gardocki, 1972; Hirshkovitz, 1979; Rosekind, Coates, & Zarcone, 1979), when vivid dreaming is more likely to occur.

If such visuospatial functions as dream imagery production are, indeed, lateralized to the right hemisphere during REM sleep they may become functionally disconnected from left hemisphere linguistic functions at this time. This notion reflects the common observation that dream mentation is frequently difficult to recall and verbally report and the experimental finding in cats that transfer across neural pathways in the corpus callosum is attenuated during REM sleep (Berlucchi, 1965). The notion is also consistent with the finding that dream recall is poor after surgical disruption of the corpus callosum. Specifically, dream recall in epileptic patients is reduced following either complete callosotomy (Bogen, 1969) or partial anterior or posterior callosotomy (Montplaisir, Côté, Laverdiere, & St. Hilaire, 1985). Reduced dream recall following anatomical disconnection of the hemispheres is thus analogous to what may be a less extreme form of "functional callosotomy" occurring during normal REM sleep.

On the other hand, what may be referred to as the *functional connection* perspective proposes that interhemispheric transfer during REM sleep is augmented, not diminished. There is, in fact, research that challenges both the notion of right hemisphere specialization (e.g., Antrobus, 1987; Greenberg & Farah, 1986; Kerr & Foulkes, 1981; Murri, Stefanini, Bonanni, Cei, Navona, & Denoth, 1984b) and the notion of hemispheric disconnection during sleep (e.g., Greenwood, Wilson, & Gazzaniga, 1977). Of particular relevance to this approach are studies using measures of EEG coherence that suggest that interhemispheric coordination is enhanced in REM sleep relative to NREM sleep. Studies on human infants indicate that during active sleep measures of interhemispheric EEG coherence are higher than in quiet sleep (e.g., Kuks, Vos, & O'Brien, 1988; Willekens, Dumermuth, Duc, & Mieth, 1984). In adults, increases in interhemispheric coherence during REM sleep have been reported for some EEG frequency bands (Dumermuth, Lange, Lehmann, Meier, Dinklemann, & Molinari, 1983; Dumermuth & Lehmann, 1981), although there is some doubt as to the consistency of such findings (Banquet, 1983; Dumermuth & Lehmann, 1981).

The prior studies are noteworthy because there is preliminary evidence that EEG coherence is a valid measure of interhemispheric connectivity (Montplaisir, Nielsen, Côté, Boivin, Rouleau, & Lapierre, 1990). The latter research showed that EEG coherence is significantly reduced after surgical section of the corpus callosum, especially over those portions of the two hemispheres specifically innervated by fibers sectioned in the partial callosotomy procedure. Taken together, this research suggests that hemispheric connectivity—as measured by EEG coherence—may increase during certain stages of sleep relative to wakefulness.

To further explore these two perspectives on hemispheric connectivity during sleep—specifically, to determine whether interhemispheric cortical processes become more or less connected during REM sleep relative to other states of the sleep/waking cycle—we sampled and compared mean EEG coherence values obtained from stage REM, stage 2, and stage 3/4 periods of sleep and from a period of relaxed, eyes-closed wakefulness.

Hemispheric dominance and sleep. The differential activation of left and right hemispheres during sleep may be mediated by the relative hemispheric dominance or "handedness" of the individual (Murri et al., 1984b). Some studies are consistent with the position that the nondominant hemisphere is relatively more active in REM sleep than in either NREM sleep or the waking state. Analyses of relative EEG power during various stages of sleep and wakefulness (Murri et al., 1984b) indicate a relative increase in activity in the nondominant (right) hemisphere for right-handed subjects, and a relative decrease for left-handed subjects. Finally, a study of the waking EEG (Shaw, O'Connor, & Ongley, 1977) demonstrated that on verbal or spatial tasks α band coherence between Fz–P3 and Fz–P4 leads increased in most right-handed subjects and decreased in most left-handed subjects.

To further examine this relationship between hemispheric dominance and sleep, and, in particular, to examine whether EEG coherence across the sleep/wakefulness cycle differs for left- and right-handed subjects, we selected samples of both left- and right-handed subjects for all-night laboratory recording of the EEG.

Gender differences and sleep. Brain activity during sleep may also be mediated by subject gender, an hypothesis suggested by McGlone's (1980) review of sex differences in brain asymmetry. She concluded tentatively that male brains are more functionally asymmetric than female brains; for example, clinical studies suggest that there is greater dependence on the left hemisphere for verbal functions in men than in women. Men and women may thus demonstrate different patterns of left–right hemispheric connectivity across the sleep/wakefulness cycle.

METHOD

Six left-handed (mean age = 26 ± 4.0 years) and six right-handed (mean age = 27 ± 5.7 years) university students reporting no history of sleep disorders, no neurological conditions, and no use of psychotropic medications were selected to participate in this research. Subjects were solicited by advertisements posted on a local university campus; one subject was contacted in a local shop specializing in products for left-handed persons. Hand preference was determined using the test of manual dominance of Crovitz and Zener (1962) and by the requirement that left-handed subjects report having at least one immediate family member (i.e., parents, siblings) who is also left-handed.[1] Each of the two manual dominance subgroups was composed of three males and three females matched for age.

Sleep was recorded and scored according to the standard method of Rechtschaffen and Kales (1968). EEG data was obtained using five electrodes placed symmetrically over each hemisphere according to the 10–20 system (Jasper, 1958). EEG data were analyzed from this system according to the parasaggital montage, which reflects cortical activity in each of the adjacent electrode pairs along the anterior–posterior axis (e.g., left side: Fpl–F3, F3–C3, C3–P3, P3–O1). EEG channels were amplified and low-pass filtered at 50 Hz with Grass Model 7P511 amplifiers, and sampled at a rate of 200 Hz and stored on digital tape by a Compaq 386 personal computer. Power spectral analysis and smoothing of each channel was performed for each of four frequency bands with a commercially available software package for EEG spectral analysis (RHYTHM, 1989). Frequency bands were defined as follows: δ (0.5–4.0 Hz), θ (4.0–8.0 Hz), α (8.0–13.0 Hz), and β (13.0–22.0 Hz).

Autospectra functions for each channel were calculated on 20 nonconsecutive 2.56-sec epochs (total time = 60 sec) and weighted by a Hamming Window. Samples were recorded for the waking state (eyes closed), and for epochs of sleep stages 2, 3/4, and REM, all of which had been manually selected to be free from eye-movement and other muscle

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[1] Subjects were also tested for handedness using a visual gaze task and a dichotic listening task (Bryden & Sprott, 1981), but these tasks did not produce a significantly different grouping of subjects. Specifically, of the six subjects classified as left-handed on the manual dominance task, five were also classified as left-handed on the visual gaze task, and four were classified as left-handed on the dichotic listening task. Of the six subjects classified as right-handed on the manual dominance task, one did not complete the other dominance tasks, four were classified as right-handed on the visual gaze task, and four were classified as right-handed on the dichotic listening task. These groupings did not produce a pattern of results in the data significantly different from those reported below for the grouping based on the manual dominance task.

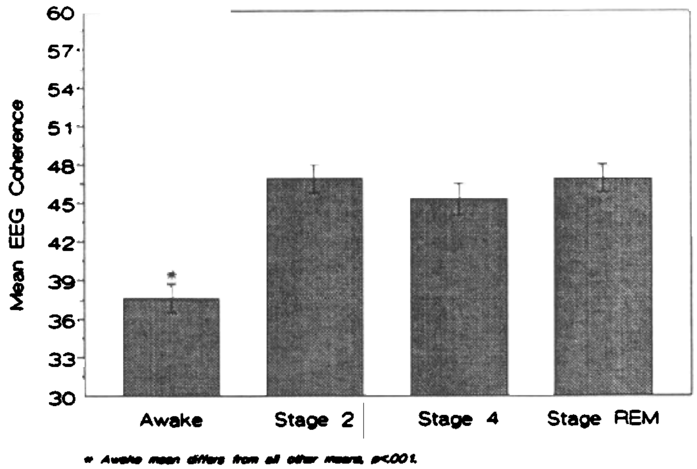

FIG. 1. Interhemispheric EEG coherence by sleep stage. *, Awake mean differs from all other means; $p < .001$.

artifact using the screen display and data selection features of the RHYTHM software. Interhemispheric coherence functions were calculated for each frequency band for each pair of homologous brain locations. A measure of mean EEG coherence was then calculated as the mean coherence of the four frequency bands (i.e., Mean EEG Coherence = $(\delta + \theta + \alpha + \beta)/4$) for each stage for each subject.

Statistical differences in Mean EEG Coherence were assessed using MANOVA designs (BMDP4V) with two between-groups factors: Hand Preference (left, right) × Gender (female, male), and two repeated measures factors: Sleep Stage (wakefulness, stage 2, stage 3/4, stage REM) × Electrode Placement (frontal, central, parietal, occipital). Because of the small size of the subject sample, results from the Hand Preference × Gender interactions were not considered in any analyses. MANOVAs were calculated using Mean EEG Coherence as the dependent measure. Differences and interactions of interest among repeated measures factors were subsequently determined using BMDP4V planned univariate contrasts. Also, the small sample size necessitated that interactions among the two repeated measures be assessed using a pooled univariate estimate of F; *df* for these tests were thus reduced by the BMDP Geisser–Greenhouse Imhof formula to correct for the liberal estimate of F provided by the pooling procedure.

RESULTS

Interhemispheric coherence as a function of sleep stage. Mean EEG coherence was found to vary as a function of Sleep Stage ($F(3, 6) = 12.28$, $p = .0057$; see Fig. 1). This large effect was due to the fact that Mean EEG Coherence during wakefulness was significantly lower than during stage 2 sleep ($F(1, 8) = 41.84$, $p = .0002$), stage 3/4 sleep ($F(1, 8) = 30.74$, $p = .0005$), and stage REM sleep ($F(1, 8) = 44.83$, $p = .0002$).

However, this Sleep Stage difference was qualified by a significant

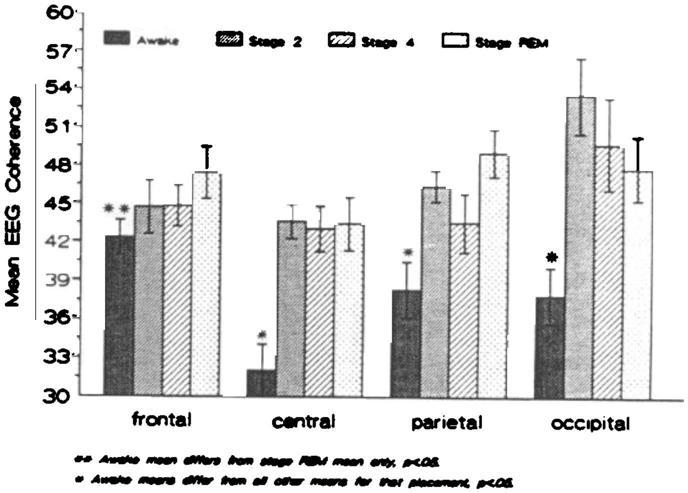

FIG. 2. Interhemispheric EEG coherence by sleep stage and electrode placement. **, Awake mean differs from stage REM mean only; $p < .05$. *, Awake means differ from all other means for that placement; $p < .05$.

interaction with Electrode Placement ($F(3, 27) = 4.29$, $p = .0109$)[2] indicating that the difference varied from anterior to posterior regions of the cortex. Specifically, univariate contrasts revealed that Mean EEG Coherence for wakefulness was significantly lower than it was for stages 2, 3/4, and REM sleep for each of the central (p = .0012, .0001, .0002, respectively), parietal (p = .0688, .0061, .0005), and occipital (p = .0020, .0001, .0002) placements, but was only significantly lower than coherence for stage REM sleep for the frontal placements (p = .2425, .3163, .0430; see Fig. 2).

Hemispheric dominance and sleep. A main effect for Hand Preference was not observed for Mean EEG Coherence ($F(1, 8) = 1.00$, $p = .3466$). However, a significant interaction between Hand Preference and Electrode Placement ($F(3, 6) = 5.07$, $p = .0439$) indicated that Mean EEG Coherence varied by cortical region differentially for left- and right-handed subjects. Specifically, values for left-handed subjects were significantly higher than those for right-handed subjects for occipital placements ($F(1, 8) = 7.74$, $p = .0238$), but not for frontal ($F(1, 8) = 0.00$, $p = .9973$), central ($F(1, 8) = 0.05$, $p = .8300$), or parietal ($F(1, 8) = 0.03$, $p = .8759$) placements (see Fig. 3). Moreover, this difference in occipital coherence obtained for wakefulness ($F(1, 8) = 11.44$, $p = .0096$), stage 2 sleep ($F(1, 8) = 6.08$, $p = .0392$), and stage REM sleep

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[2] Degrees of freedom for the Sleep Stage × Electrode Placement interactions are adjusted by the Geisser–Greenhouse Imhof correction factor.

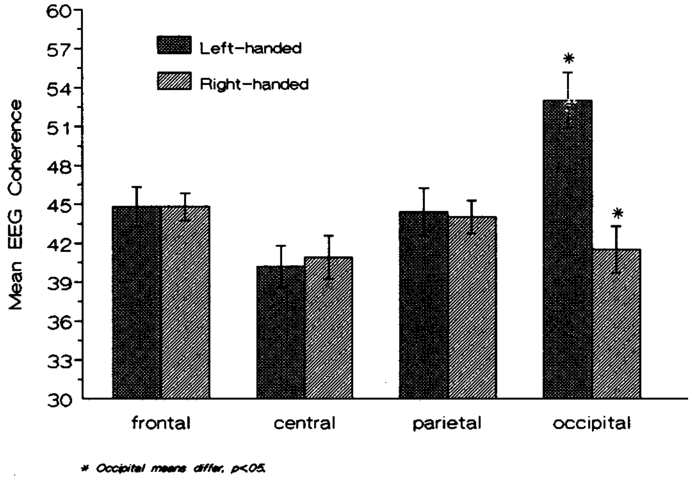

FIG. 3. Interhemispheric EEG coherence by handedness and electrode placement. *, Occipital means differ; $p < .05$.

($F(1, 8) = 14.97$, $p = .0047$), but not for stage 3/4 sleep ($F(1, 8) = 2.07$, $p = .1880$).

The latter Hand Preference × Electrode Placement interaction also accounts for an observed main effect for Electrode Placement ($F(3, 6) = 7.08$, $p = .0214$) which indicated overall higher Mean EEG Coherence for occipital placements.

Gender and sleep. No main effect for Gender was found on the Mean EEG Coherence measure ($F(1, 8) = 0.06$, $p = .8089$), nor were any interactions with Gender found to be statistically significant.

No other statistically significant main effects or interactions among variables were found for these analyses.

DISCUSSION

Functional interhemispheric connection in REM sleep. The present results provide no strong support for either the functional disconnection or the functional connection perspectives. There is definitively no evidence that interhemispheric coherence decreases during REM sleep relative to wakefulness. Coherence values during REM sleep were in all cases found to be larger than coherence values during wakefulness. On the other hand, our results also do not show that these increases in EEG coherence are selective to REM sleep. Rather, relative to wakefulness, interhemispheric coherence was found to be elevated during all stages of sleep.

Our results are thus in general terms consistent with other studies that have shown increases in EEG coherence during both REM and NREM sleep relative to the waking state (Dumermuth & Lehmann, 1981; Dumermuth et al., 1983). However, they do not replicate previous findings that EEG coherence is further augmented during REM sleep relative to NREM sleep (Dumermuth & Lehmann, 1981; Dumermuth et al., 1983) or that interhemispheric coordination increases during REM sleep relative to NREM sleep as measured either by interhemispheric correlation (Barcaro, Bonanni, Denoth, Murri, Navona, & Stefanini, 1989; Corsi-Cabrera, Meneses, & Molina, 1987) or single unit electrode implants (Moiseeva, 1979).

However, it should be noted that Dumermuth et al. (1983) found that EEG coherence increased during REM sleep only in certain frequency bands; we did not report differences for individual frequency bands. It is also noteworthy that the Dumermuth group recorded their EEG samples with all electrodes referenced to Cz; our electrodes, by contrast, were referenced to linked-ear electrodes. Another reason for the relative lack of difference between stage 2 and stage REM coherence in our study may be that our manual screening of EEG epochs containing bursts of eye movements diminished the degree of coherence attributable to eye movement generation in stage REM. This suggestion stems from a previous exploratory study of interhemispheric EEG coherence during REM sleep with and without eye movements, which showed that coherence was higher during eye movement bursts, even in posterior channels, which are relatively unlikely to be affected by eye movement artifact (Dionne, 1986). The suggestion that heightened interhemispheric coherence during REM sleep is due to factors associated with eye movement generation is also consistent with the finding that fibers of the cat corpus callosum are active during REM sleep with eye movements but not during REM sleep without eye movements (Berlucchi, 1965).

The present findings for Sleep Stage suggest that changes in EEG coherence reflect general changes in brain processes associated with the alternation between sleep and wakefulness, but they do not necessarily reflect more specific changes in processes associated with the alternation of brain processes through stages 2, 3/4, and REM sleep. Since previous research suggests that higher levels of interhemispheric coherence may reflect greater levels of interhemispheric coordination (Montplaisir et al., 1990), the present findings point to the possibility that sleep, in general, is characterized by a tonic background state of heightened brain coordination or interconnection relative to relaxed, eyes-closed wakefulness. Whether systems responsible for the eye movement bursts of REM sleep add a second, phasic increase in coherence to this background state is a question requiring further research; studies of coherence during REM sleep have generally not considered the effect of eye movement generation processes on EEG coherence.

Hemispheric dominance and sleep. The present findings for Hand

Preference do not confirm previous demonstrations that EEG coherence is lower in left-handed than in right-handed subjects (Shaw et al., 1977). Rather, they indicate that occipital EEG coherence in left-handed subjects is relatively higher than in right-handed subjects during some stages of the sleep/wakefulness cycle.

This pattern suggests that among left-handed persons there may exist greater interhemispheric coordination in posterior brain regions—possibly due to some increased demand for visual information processing in occipital areas. The pattern may even mean that among left-handed subjects selectively there is a greater degree of right-to-left communication from visuospatial (right hemisphere) to verbal-linguistic (left-hemisphere) brain regions. In waking states, such activity may coordinate visuoverbal productions such as writing or drawing. For example, one study of handwriting posture consistent with the present finding found that EEG asymmetry over occipital leads but not over central and parietal leads varied with the habitual handwriting posture of left-handed subjects performing cognitive tasks (Herron, Galin, Johnston, & Ornstein, 1979).

In dreaming states, including especially stages 2 and REM sleep for which recall of "dreamlike" content is frequent, occipital coherence may also reflect the right-to-left flow of information from visuospatial regions to verbal–linguistic regions. A case reported by Kerr and Foulkes (1981) suggests that the visuospatial and verbal–linguistic aspects of dreaming are generated independently and then integrated via temporal and occipital pathways. These researchers found that right hemisphere damage to temporal and occipital pathways can eliminate visuospatial elements of dreaming while leaving structures responsible for narrative organization intact. In the case of left-handed subjects, then, greater occipital coherence may reflect greater integration of information from the two hemispheres, both of which are necessary for the final production of dreaming.

These considerations suggest that the dream processes of left-handed subjects may differ in some fashion from those of right-handed subjects. Some data indeed demonstrates a difference in habitual dream recall ability, but in a direction opposite to what might be predicted if the present results are taken to support the functional connection perspective. In particular, left-handed subjects recall *less* content on a home dream collection task than right-handed subjects (Violani, DeGennaro, & Solano, 1988).

Another possible explanation of the present results for Hand Preference is that the augmented occipital EEG coherence observed for left-handed subjects reflects a greater demand for interhemispheric processing resources rather than a greater degree of functional connection per se. For example, it has been proposed that left-handed persons are more ambilateral in the cerebral organization of visuospatial abilities than are right-handed persons, i.e., they show less marked hemispheric localization of visual processes (cf., Hecaen & Sanguet, 1971), and thus perform more poorly than right-handed subjects on visuospatial tasks (Buffery, 1974; Levy, 1972).

Whether heightened occipital coherence among left-handed persons proves to reflect interhemispheric integration or ambilateral cerebral organization, further research is clearly warranted for the clarification of possible relationships between brain organization and associated visual imagery processes in left- and right-handed subjects. The present findings suggest that differences between left- and right-handed subjects should be found on processes associated with both wakefulness and stages 2 and REM sleep, processes such as those involved in the production of visuospatial imagery.

Gender and sleep. The present study found no gender difference for interhemispheric coherence. This finding fails to confirm the general suggestion that males show greater functional asymmetry than females (McGlone, 1980) and is more consistent with criticisms of McGlone's conclusions (e.g., Annett, 1980; Fairweather, 1980). Rather, the increase in EEG coherence for stages 2, 3/4, and REM sleep over relaxed wakefulness was found to be equally robust for both male and female subjects. However, further work should evaluate possible interactions between gender and hand preference in assessing the generality of this finding.

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