Night-time right hemisphere superiority and daytime left hemisphere superiority: A repatterning of laterality across wake–sleep–wake states

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Abstract

During the sleep onset period (SOP), there is a state-specific relative advantage of the right hemisphere (RH). This superiority could either be due to the ability of the RH when operating at levels of reduced arousal, as suggested by its superiority in sustaining vigilance, or it could depend on a more pronounced homeostatic deactivation of the left hemisphere (LH). To evaluate whether variations of lateralization from wake to sleep are consistent with one of these two hypotheses, we considered a finger tapping task (FTT) bimanually performed during two wakeful conditions, during the SOP, upon experimental awakenings from stage 2 and REM sleep in the first and in the second part of the night, and upon morning awakening. The RH advantage in sustaining vigilance would be supported if the relative RH advantage was present throughout the sleep period. Finding that the repatterning of hemispheric asymmetry is present and/or prominent in the first part of the night would support the homeostatic hypothesis, i.e. when the homeostatic process is more pronounced. Results from 16 subjects revealed a significant superiority of the LH during the two wakeful conditions. At sleep onset, a clear reversal of dominance was observed and it was followed by a steady RH superiority upon both REM and NREM sleep awakenings, and upon the morning sleep–wake transition. Therefore, performance in a FTT reveals a repatterning of laterality across wake–sleep–wake states. These results are interpreted as consistent with the hypothesis concerning an advantage of the RH in sustaining vigilance.

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1. Introduction

Using behavioral techniques, it was found that there are systematic variations of hemispheric functioning when falling asleep (Casagrande et al., 1995b). A stronger impairment of the LH both in reacting to external stimuli (auditory reaction time task) and in sustaining endogenous motor programs (FTT), suggested a repatterning of hemispheric asymmetry in the SOP, considering the LH superiority during the wakeful condition (e.g., Patterson and Bradshaw, 1975). During the transition from wakefulness to sleep, the right-hand (left hemisphere) stops responding before the left (right hemisphere) both in the reaction time task and in the FTT, showing that the left hemisphere falls asleep earlier than the right hemisphere. This variation in behavioral hemispheric pattern is in line with the one shown by EEG techniques. Sleep onset happens at different times in the two hemispheres also when considering both EEG (i.e. appearance of visually detected theta rhythm) and behavioral (i.e. stopping of hand responses in a FTT) measures (Casagrande and Bertini, 2007). Furthermore, in the first minute of stage 1 a significant decrease of interhemispheric coherence was found for the EEG alpha and beta rhythms in the frontal and temporal cortical areas (Wright et al., 1995), that are consistent with other EEG data (Boldyrev and Zhavoronkova, 1991; Zhavoronkova and Trofimova, 1997, 1998), indicating a right hemisphere dominance during sleep onset.

Two hypotheses have been proposed to explain the behavioral shift of hemispheric asymmetries during the SOP. Based on the first, shifts in hemispheric activation from wake to sleep are interpreted as due to a greater restorative need for the left hemisphere. This homeostatic hypothesis proposes that, since the left hemisphere is more active during waking, it may
have a greater increase in the sleep debt compared with the right hemisphere and, therefore, it falls asleep more quickly than the right hemisphere. Consistent with this view are data showing that unilateral activation of the left somatosensory cortex during wakefulness results in an increase of EEG power density in the delta frequency in the left hemisphere during the first hour of subsequent sleep (Kattler et al., 1994), but also with EEG data showing an EEG frontal right hemisphere dominance after sleep deprivation (Achermann et al., 2001).

According to the second hypothesis, hemispheric shifting during the SOP is explained by the right hemisphere advantage in sustaining vigilance (Raz, 2004; Sturm et al., 1999; Weis et al., 2000; Whitehead, 1991).

To evaluate whether variations of lateralization from wake to sleep are consistent with one of these two hypotheses, we considered a FTT bimanually performed during different moments of the wake–sleep cycle; namely, the FTT was applied during an evening wakeful condition, in the early and the last part of the SOP, upon experimental awakenings from stage 2 and REM sleep in the first (second cycle NREM–REM) and in the second part of the night (third and fourth cycle NREM–REM), upon morning awakening, and during a morning wakeful condition.

Finding that the repatterning of hemispheric asymmetry is present and prominent in the first part of the night would support the homeostatic hypothesis, i.e. when the homeostatic process is more pronounced (Borbely, 1982). During the night these changes in hemispheric asymmetries should decrease until they restore the usual wake hemispheric asymmetry, when the sleep debt of the left hemisphere is exhausted. The hypothesis of a right hemisphere advantage in sustaining attention would be supported if the relative left-hand advantage, already observed in the transition from wake to sleep (Casagrande and Bertini, 2007; Casagrande et al., 1995b, 1999) was present throughout the sleep period.

The vigilance hypothesis would be further supported by finding that right hemisphere superiority increases more when sleepiness increases. Specifically, a faster performance of the left-hand with respect to the right would be present when the sleepy brain exhibits longer inter-tapping intervals (ITI), the latter being significantly affected by sleepiness (Casagrande et al., 1997).

2. Method

2.1. Subjects

Sixteen male undergraduates, aged 20–27, signed an informed consent before participating as paid volunteers in the study. The participants were selected as being strongly right-handed, with a hand preference $\geq 95$, as assessed by a lateral preference questionnaire (Salmon and Longoni, 1985). For 1 week, subjects were required to fill in a sleep diary at home daily upon morning awakening. Only subjects that reported normal sleep duration (7:30–8:30 h/day) and schedule (going to sleep at 11:30 p.m. $\pm 60$ min and waking up at 7:30 a.m. $\pm 60$ min) and who reported no sleep, medical, or psychiatric disorders were included in the study. Finally, the subjects were all drug free and themselves were unaware of the purpose of the experiment.

2.2. Polygraphic recordings

A “Beckman R 611” polygraph set at a paper speed of 10 mm/s was used for polygraphic recordings.

The EEG activity was recorded from electrodes fixed to the scalp at central, frontal and occipital locations over each hemisphere. EEG recordings were unipolar (C3-A2, C4-A1, F3-A2, F4-A1, O1-A2, O2-A1) with a time constant of 0.3 s. Bipolar horizontal eye movements were recorded from electrodes placed about 1 cm from the medial and the lateral canthi of the dominant eye; bipolar vertical eye movements were recorded from electrodes located 3 cm above and below the right eye pupil. Both were recorded at a time constant of 1 s. Submental electrodes were employed for recording bipolar EMG, with a time constant of 0.03 s. All recordings were in AC.

Central EEG (C3-A2), EMG and horizontal and vertical EOGs were used to visually score sleep stages using the standard Rechtschaffen and Kales criteria (Rechtschaffen and Kales, 1968).

2.3. Finger tapping task

The FTT required bimanual responses to be given by using the index finger to press the button on a cylindrical paddle connected to the game I/O of an Apple IIe. The switch had a closure distance of 3 mm. Subjects were required to press the button as quickly as possible, but with a tapping rate compatible with performing for several minutes without getting tired.

To avoid that subjects could lose and/or reverse paddles when falling asleep, these were secured by tape to the palm of each hand. The task was controlled by an Apple IIe personal computer, which recorded the inter-tapping intervals and the times from light out to each ITI, for each hand. During the SOP and upon awakening from REM and stage 2 sleep, data were recorded for 1 h from light out or until stage 3 was scored for at least 1 min. During the wakeful condition (in morning and evening periods) and upon morning awakening, data were recorded for 14 min.

2.4. Procedure

Subjects spent three consecutive nights each in a sound attenuated air-conditioned sleep-room. Each subject came to the Sleep Lab the afternoon before the first night of the study (which was for adaptation) and received instructions on the experimental procedures. On the second night (at 19:30), subjects were tested to assess their wake performances in the FTT. In this wakeful condition, the FTT lasted 14 min. This duration was chosen to see whether shifts in performances during the SOP depended on hemispheric variations or on fatigue. Then, after electrode montage, subjects were required to fall asleep bimanually performing a FTT. Sleep onset was at 23:30, ranging from 23:00 to 24:00. They were awakened twice during the night, once from REM and once from NREM (stage 2) sleep; eight subjects were awakened 5 min after the beginning of the second NREM period and 5 min after the onset of the third REM period. The other eight subjects were first awakened 5 min following the onset of the second REM and 5 min after the onset of the fourth NREM. Upon each awakening, subjects were again required to fall asleep bimanually performing a FTT. Upon final awakening (at 7:30) subjects were required to perform a FTT lasting 14 min and, finally, during the morning (at 10:30 about), they once more performed a FTT lasting 14 min. On the third night, subjects were submitted to an identical procedure, varying only the order of awakening from REM and NREM sleep, which was counterbalanced across the subjects. During sleep onset, REM, NREM and final awakening conditions, the FTT was performed in the dark with the subject lying on the bed; in wakeful conditions, the FTT was performed under a dim light with the subject sitting on a chair in one wakeful condition and lying on the bed in the other one.

2.5. Data analysis

Central EEG (C3-A2), EMG, and horizontal and vertical EOGs were used to score sleep stages, using the standard Rechtschaffen and Kales (1968) criteria.

For each hand, the behavioral sleep onset latency was computed using as a behavioral definition of sleep: “failures to press for at least 20 s”. The duration of the behavioral SOP was defined as the time lapse beginning at light-out time.
To assess variations in behavioral response of the right- and left-hand during the SOP, two stages were defined; each of them lasted 20 s. The first stage included the first 20 s after lights out (early SOP: ESOP); the second stage included the last 20 s in the SOP (late SOP: LSOP). To evaluate the performance of the right- and left-hand upon awakening from stage 2 and REM sleep, the first 20 s after awakening were considered. For final awakening, two stages were considered: the first (first part of final awakening: FPFA) and the last (last part of final awakening: LPFA) 20 s of the right- and the left-hand performance. Finally, the first and the last 20 s of both the right- and the left-hand performance were considered for the two wakeful conditions.

Dependent variables were the mean ITI. To eliminate the key-bounce artifact, any ITI of less than 100 ms was excluded from the analysis.

All the data were submitted to natural logarithmic transformation.

Since the mean ITI recorded during wakeful conditions were incomparably faster as compared to those recorded during sleep onset and upon stage 2, REM sleep and final awakenings, the data were analyzed by separate ANOVAs as a function of the condition (wake–sleep).

3. Results

3.1. FTT performance during wakeful conditions

To see whether hand performance was affected by time of day and by task fatigue, mean FTT in the first and in the last 20 s of awake performance were submitted to Time of day (morning versus evening) by Part (first 20 s versus last 20 s) by Hand (right versus left) ANOVA. ANOVA showed only a significant effect for the Hand factor (F1,15 = 22.60; p < .001), indicating faster ITI for the right-hand (mean = 5.59 ln (ms); S.D. = ±1.75) as compared to the left-hand (mean = 5.72 ln (ms); S.D. = ±1.97).

Fig. 1 shows left- and right-hand performance for every state.

Pearson correlations were used to evaluate whether a relationship between the relative superiority of the left-hand in FTT performance and the decrease of vigilance was present. For each state (wakeful conditions, SOP, NREM, REM, and morning awakening) left and right ITI differences (left minus right) were computed and correlated with the mean performance scores (mean of the right ITI + mean of the left ITI). As shown in Tables 1 and 2, positive correlations were present during the wakeful condition, while negative correlations were found for each other state when between and within subject conditions were considered. In other words, the subjects who show the general (right- plus left-hand) poorer performances are those who show the higher hands differences in favor of the left-hand; and this is true for either the wake and the transitional wake–sleep and sleep–wake states.

4. Discussion

During the awake condition before sleep a significant superiority of the left hemisphere was observed. A clear reversal of dominance at sleep onset was followed by a steady right hemisphere advantage upon awakening from both REM and NREM sleep, and in the sleep–wake transition. A left

![Graph showing ITI (ln msec) for right and left hand during wakeful conditions, SOP, NREM, REM, and morning awakening](image)
hemisphere dominance is again established in the following wakeful state.

The bimanually performed FTT is used to reveal hemispheric asymmetries in the awake state: a functional superiority of one hemisphere being indicated by faster responses of the controlateral hand (Patterson and Bradshaw, 1975). In this study, performance in the FTT confirms our previous findings on the shift in hemispheric asymmetry during the sleep onset period (Casagrande and Bertini, 2007; Casagrande et al., 1995b, 1999) and reveals a general repatterning of laterality across the awake–sleep–wake states. The greater advantage of the right hemisphere was found during the two transitional states: the last part of the SOP and the last part of the final awakening period. Thus, our data shows that functional interhemispheric asymmetries can vary across different levels of vigilance and from wake to sleep. By analyzing the coherence of EEG during the transition from wakefulness to sleep, other studies have found a decrease in interhemispheric asymmetry during sleep onset (Wright et al., 1995; Boldyrev and Zhavoronkova, 1991; Zhavoronkova and Trofimova, 1997, 1998). In fact, during the sleep onset period, all bands, except beta, reverse to predominate in the right hemisphere (Boldyrev and Zhavoronkova, 1991; Zhavoronkova and Trofimova, 1997, 1998). Furthermore, in the centro-parietal 4–8 Hz band a right hemispheric predominance in NREM sleep has been described and it was above all prominent in the first hour of sleep (Roth et al., 1999).

Our results show an early and more pronounced decrease of vigilance for the left hemisphere following other hemispherical data on vigilance. In a lexical decision task, the rate of decrease in response accuracy is greater for stimuli presented to the right visual field than to the left visual field (Babkoff et al., 1985). In lateralized vigilance tasks the left hemisphere, as compared to the right, has most false positives (Dimond and Beaumont, 1971). Finally, on a vigilance task, the left hemisphere only shows a continuous decrease of performance throughout the task. No general negative trend is shown over the experimental period by the right hemisphere. This finding suggests that the left hemisphere plays a different role in some ways from the right in the vigilance process (Dimond and Beaumont, 1973). Data from split-brain patients, suffering from a decrease in vigilance, are in line with this; an impairment probably due to failure of the alerting action of the right hemisphere on the left (Dimond, 1979).

Dimond and Beaumont (1971) suggested the presence of two vigilance systems within the brain: a primary system operating initially at a high level, showing a decrease over time and associated with the left hemisphere, and a secondary system showing no decrease, but operating at a lower level, associated with the right hemisphere. Our data seem to confirm this view. Blood flow data obtained from a normal population similarly show right hemisphere superiority in the control of vigilance. Both tactile (Risberg and Prohovnik, 1983) and kinesthetic stimuli (Halsey et al., 1979) administered on the left-hand cause a greater increase of cerebral blood flow than those administered on the right-hand. The right midfrontal cortex was found to be more active during an auditory discrimination task (Cohen et al., 1988) and this region, as well as the right superior parietal cortex, also turned out to be more active in both visual and somatosensory vigilance conditions (Pardo et al., 1991). Finally, in normal subjects, regional cerebral blood flow showed a greater activation of the anterior right hemisphere when performing visual vigilance tasks (Bench et al., 1993; Deutsch et al., 1988; Raz, 2004; Sturm et al., 1999; Weis et al., 2000).

By using behavioral tasks, a right hemisphere superiority upon awakening from REM sleep was found (Gordon et al., 1982; Bertini et al., 1984; Casagrande et al., 1995b). Similarly, Chong-Hwa Hong et al. (1995) detected a lateralized cerebral glucose metabolism during REM sleep, suggesting a right hemisphere specialization in saccadic eye movement control during REM sleep. Recent EEG data confirm a shifting of laterality from wake to sleep, showing a waking left prefrontal dominance and a REM sleep right frontonal dominance (Boldu...
et al., 2003). These data are consistent with results by Droste et al. (1993) who found a tendency toward a higher blood flow velocity during REM sleep on the right side than on the left side. However, no hemispherical differences in regional cerebral blood flow during REM sleep have been found in other studies (Braun et al., 1998; Maquet and Phillips, 1998), except for a greater activation of the left thalamus and right parietal operculum (Maquet et al., 1996).

Finally, the significant correlation between the right hemisphere advantage and the decrease of vigilance suggests a new functional superiority for the right hemisphere: the monitoring of the environment when people are in a drowsy or sleep state and therefore more vulnerable to external stimuli, a hypothesis that can be easily submitted to further testing.

The main finding of our research is the demonstration of an inversion of brain hemisphere dominance from wake to sleep to wake in a widely known psychomotor task. In fact, although the present data were collected during the sleep onset period and upon awakening from different sleep states, several findings converge in legitimizing the assumption that differences can be attributed to the physiology of the sleep state preceding awakening: (1) the 30-min interval to fully reestablish wake regional brain activity patterns upon awakenings from sleep as revealed by both PET (Balkin et al., 2002) and blood flow velocity (Hajak et al., 1994) studies; (2) the results of studies on interhemispheric asymmetries during sleep by post-awakening behavioral assessment (Bertini et al., 1984; Casagrande et al., 1995a; Gordon et al., 1982); (3) the well-known stage effect on sleep inertia measures, that has greater negative effects on subsequent performance after slow wave sleep awakenings than REM sleep awakenings (Tassi and Muzet, 2000); and (4) the coherent pattern of motor threshold changes in response to magnetic stimuli delivered upon REM and NREM awakenings (Bertini et al., 2004).

Neural control of finger tapping movements depends on central pre-programming (Schmidt, 1975) and peripheral factors are relatively unimportant in producing between-hand performance differences in tapping (Peters, 1980). Furthermore, there is considerable support for the hypothesis that assigns a central role to attentional factors in the coordination of bimanual activities (Peters, 1985). Recently, motor behavior was evaluated by contrasting two-finger tapping (in-phase and anti-phase) during bimanual and unimanual conditions (Serrien, in press). To evaluate the neural activation patterns, the data analysis in this study focuses on EEG coherence that expresses functional interactions between brain areas (e.g., Blum et al., 2007). Results from this study showed that interhemispheric coupling strength differed for unimanual and bimanual coordination. The lowest EEG (beta rhythm) coherence scores were observed for bimanual in-phase movements. In particular left hemisphere dominance for bimanual and right-hand coordination versus right hemisphere dominance for left-hand coordination was present. For the author these results support the view that bimanual in-phase coordination comprises a lower-level mode in contrast to unimanual movements that require increased interhemispheric communication, possibly to prevent the opposite hemisphere from interfering with the required behavior.

In conclusion, performance in the FTT of each hand can be without doubt considered as an indicator of controlateral hemispheric activation.

Our data confirm the ability of the right hemisphere in operating at reduced arousal levels (Babkoff et al., 1985; Casagrande et al., 1995a; Dimond and Beaumont, 1971, 1973), in accordance also with other data showing an increased activation in the prefrontal cortex and parietal lobes, particularly in the right hemisphere, following total sleep deprivation (Drummond et al., 2001; Szelemenberger et al., 2005).

We found a right hemisphere superiority when the brain is sleepy and when the vigilance system has to monitor for potential warning stimuli. These results are in keeping with data showing the advantage of the right hemisphere in the control of vigilance (e.g., Posner and Rafal, 1987) and in responding to warning stimuli (e.g., Hellman and Van Den Able, 1980). In other words, the right hemisphere seems to maintain a “wakeability” or “vigilanceability” also when the brain is going to sleep. This advantage seems to be an important biological requirement for an adequate environmental adaptation. Right hemisphere superiority during both drowsiness and sleep states may be useful for the cognitive system, when it is operating in a relative absence of external input and of voluntary control of the stream of thoughts. A decrease of left hemisphere vigilance, with respect to the right, could enable a hierarchical reorganization of cognitive mechanisms, functional to a mental activity that is different from the one typical of the wakeful condition, i.e. a change in hierarchical integration, from LH to RH, could be functional to some internally oriented operations, which are more prominent when the brain is drowsy or sleeping.

References


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