EEG LORETA and the Default Mode of the Brain

Rex L. Cannon, Robert W. Thatcher, Debora R. Baldwin and Joel F. Lubar

Abstract—INTRODUCTION: Recent research exploring cortical functional connectivity defines a default network (DNt) of brain function. The electroencephalographic activity in these components of the human DNt is not well understood. METHODS: This study was conducted with 46 participants. Individuals were recorded during eyes-closed (ECB) and eyes-opened (EOB) baselines and active task (AT) conditions (self-referential and self-image processing). We compared EEG source localization with standardized low resolution electromagnetic tomography (sLORETA) between the four conditions. RESULTS: The ECB resting condition shows higher activity in delta and theta frequencies for all ROI. Likewise, the active tasks show differential effects for increased activity as compared to EOB for each ROI in each frequency domain. CONCLUSION: The data are in agreement with other neuroimaging techniques (fMRI/PET) investigating the DNt of brain function and further shows that the 3-dimensional localization accuracy of LORETA EEG is sufficient for the study of the DNt. In examining both within and between functional core regions there is a higher degree of activity in lower frequency bands during eyes closed; however, this pattern does not extend to all ROIs in the higher frequencies. We conclude that this difference represents functional connectivity relating to endogenous/exogenous attention states as opposed to the simple concept of “resting” or “non-activity”. Further study of the functional relationships between EEG frequencies within and between the default core of the cortex may prove important to understanding the complex nature of functional integration.

I. INTRODUCTION

In the past decade neuroimaging research has demonstrated that during specific cognitive tasks the human brain exhibits increased spatial organization in neuronal assemblies [1]. The default mode network (DNt) was discovered using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) techniques. A consistent decrease in neural activity in the DNt during active tasks was measured by a local decrease in cerebral blood flow and blood-oxygenated level-dependent (BOLD). PET is a direct measure of local neuronal activity [2], such that increased neural activity increases cerebral glucose metabolism (CGM) to brain regions involved in mental activities or cognitively demanding tasks [3-5]. The fMRI BOLD response is an indirect measure of neural activity and despite the advantages of increased spatial resolution there remain limitations to the temporal resolution and ambiguity associated with the interpretation and reporting of results [6, 7]. There is often a high degree of overlap in activation of brain regions during cognitive, memory, attentional and affective tasks which adds to the difficulty in interpreting fMRI results [8]. Despite these challenges the finding of reduced activity in DNt during active tasks has been replicated in numerous studies [9-12]. Increasing knowledge of the functional dynamics of the DNt may be aided by studying the Electroencephalogram (EEG) in the DNt since it provides very good temporal resolution in milliseconds [1] and with the advent of EEG source localization techniques [13, 14] it is possible to explore EEG activity in neocortical and limbic regions associated with DNt. Low-resolution electromagnetic tomography (LORETA) and the standardized version (sLORETA) are inverse solutions that have been validated as accurate for estimating the potential sources of the scalp EEG [15-20]. However, to date the EEG activity in the DNt regions has not been investigated. The regions associated with the DNt and a priori regions of interest (ROI) for this study are shown in table 1. In the table from left to right is the orientation within the brain, (i.e., right, left, medial) and Brodmann area (BA), the x, y, and z coordinates and the neuroanatomical label. The DNt is typically associated with a ‘resting state’ which is described as an ‘idling, non-cognitive brain.’ This state is typically observed with the individual relaxing with the eyes-closed (or eyes-closed baseline). The ROIs in table 1 typically show increased activity during the baseline as compared to cognitive or working memory tasks [21, 22]. The description of ‘resting state’ in published studies is given as ‘subjects were instructed to relax with their eyes closed’ with the subjects’ confirmed report of this condition after the scans [10, 23-25]. Research has demonstrated there is decreased coherency between DNt regions in Alzheimer’s disease, especially concerning the role of the posterior cingulate and left hippocampus [26]. The posterior cingulate is suggested to be among the most metabolically active regions of the resting state networks (RSN) in healthy subjects [12]. Also, the posterior cingulate is the most highly connected neocortical
The EEG activity in these DNt structures to date has not been investigated; however, recent studies have examined correlations between EEG alpha activity [34, 35] and ultra-slow EEG frequencies (<0.01 – 0.05 Hz) with the fMRI BOLD signal [23]. Coherency between ultra-slow EEG and BOLD led to the identification of five distinct resting state networks (RSN) [23] and correlations between alpha activity and BOLD [34, 36]. If the DNt is a stable and persistent component of the human brain then it is important to understand how the healthy brain functionally communicates between assemblies of neurons in a minimally stimulated state as opposed to specific activated tasks. Such studies are important for improving our understanding of functional neural mechanisms in addition to the development of more sophisticated conceptualizations for disruptions of these mechanisms in psychopathology. The DNt like other novel concepts is not without controversy [37-39]. There is debate about what constitutes a ‘resting state’ with suggestions that it reflects internally directed mental activity [40] whereas others posit it as mind wandering [37]. The present study is designed to address four problems associated with the DNt. First, we hypothesized that it is possible to utilize 3-dimensional source localization techniques (sLORETA) to study the DNt. Second, we sought to describe functional connectivity patterns of EEG frequency domains within the DNt in both baseline and active tasks with the hypothesis that many regions will exhibit task specific increases or decreases in current source density. Third, we hypothesized that significant differences exist in current source density levels between the experimental conditions and finally, we sought to determine the subjective experience of the DNt, with the hypothesis that the subjective reports of the participants would represent attentional processes; including, attention to eye, head, jaw and body movements; attention to state of awareness, or not getting bored or drowsy; attention to the external environment and attention to thought processes as opposed to the simple concept of the described ‘resting state’.

Table I: Regions identified in the default mode of brain (DNt)

<table>
<thead>
<tr>
<th>Orientation/ Brodmann Area</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Neuroanatomical label</th>
</tr>
</thead>
<tbody>
<tr>
<td>1  Medial 3/17</td>
<td>-5</td>
<td>-49</td>
<td>40</td>
<td>Dorsal Posterior Cingulate</td>
</tr>
<tr>
<td>2  Left 40</td>
<td>-53</td>
<td>-39</td>
<td>42</td>
<td>Parietal Lobe</td>
</tr>
<tr>
<td>3  Left 19/19</td>
<td>-45</td>
<td>-67</td>
<td>36</td>
<td>Angular Gyrus</td>
</tr>
<tr>
<td>4  Right 49</td>
<td>45</td>
<td>-57</td>
<td>34</td>
<td>Parietal Lobe</td>
</tr>
<tr>
<td>5  Left lateral 8</td>
<td>-27</td>
<td>27</td>
<td>40</td>
<td>Frontal eye fields</td>
</tr>
<tr>
<td>6  Right 8/9</td>
<td>5</td>
<td>49</td>
<td>36</td>
<td>Frontal lobes</td>
</tr>
<tr>
<td>7  Left 9</td>
<td>-15</td>
<td>55</td>
<td>26</td>
<td>Dorsolateral prefrontal cortex</td>
</tr>
<tr>
<td>8  Left 10</td>
<td>-19</td>
<td>57</td>
<td>8</td>
<td>Anterior prefrontal cortex</td>
</tr>
<tr>
<td>9  Medial 10</td>
<td>-1</td>
<td>47</td>
<td>4</td>
<td>Middle frontal lobe</td>
</tr>
<tr>
<td>10 Left 10/47</td>
<td>-33</td>
<td>45</td>
<td>6</td>
<td>Inferior frontal lobe</td>
</tr>
<tr>
<td>11 Medial 32</td>
<td>3</td>
<td>31</td>
<td>-10</td>
<td>Anterior cingulate</td>
</tr>
<tr>
<td>12 Left 20</td>
<td>-49</td>
<td>-19</td>
<td>-18</td>
<td>Inferior temporal gyrus</td>
</tr>
</tbody>
</table>

Note: T1, T2, L1, L2, L3/3 not applicable in the MNI atlas utilized.

II. METHODS

2:1 Participants

This study was conducted with 70 non-clinical participants. Data inclusion was based on length of usable EEG for each file to be analyzed ≥ 60 seconds. Thus our actual sample consisted of 46 participants with an equal number of males and females with a mean age of 19.28, SD = 2.0. All participants were recruited via the University of Tennessee Human Research Participation pool and all received extra course credit for their participation. Exclusion criteria were assessed by a standard questionnaire used by our laboratory and consisted of previous head trauma, neurological or neurovascular disease, or recent drug or alcohol use (within the prior 14 days). All subjects read, signed and agreed to protocol approved by the university institutional review board.

2:2 Data Collection

Participants were prepared for EEG recording using a measure of head circumference and the distance between the nasion and inion to determine the appropriate cap size and placement for recording (Electrocap, Inc; Blom, & Anneveldt, 1982). The head was measured and marked prior to EEG recording. The ears and forehead were cleaned for recording with a mild abrasive gel (Nuprep) to remove any oil and dirt from the skin. After fitting the caps, each electrode site was injected with electrogel and prepared so that impedances between individual electrodes and each ear were < 10 KΩ. The EEG recording was conducted using the 19-lead standard international 10/20 system (Jasper, 1958). The data were collected and stored with a band pass set at 0.5–64.0 Hz at a rate of 256 samples per second using the Truscan acquisition system (Deymed Diagnostics). We utilized linked ears and ground reference with 9mm tin cups. The Electrocap was also referenced at FPz.
The participants were recorded in four conditions. First we obtained four-minute eyes-closed (ECB) and eyes-opened baselines (EOB). Participants were instructed to attempt to control eye, tongue, neck and jaw movements and to relax as much as possible during baselines. Second, the participants completed the Self-Perception and Experiential Schemata Assessment (ES) [41]. The participants observed 45 questions on Microsoft PowerPoint and responded verbally with their choice. The SPESA contains 15 items associated with each phase of human development, childhood, adolescence and adulthood. Each of the response items were presented for 8 seconds. Instructions were given to the participant prior to the stimulus presentation to read each item and each response and respond verbally with the choice (A, B, C or D) that best reflects his or her perception of self in experience, including actual experiential events (e.g., abuse, neglect). The responses were marked within the EEG record. To minimize artifacts during all EEG procedures, a 15.4 inch monitor was placed in position such that the participant was looking in a downward direction at the monitor. This tends to help minimize eye-movement artifacts and reduce reading-scanning effects. Finally, the participants were recorded while viewing a photograph of self taken prior to capping (SI). To better understand and expand upon the phenomenology of the ‘resting state’ we obtained written reports for the subjective experience of the participants during each of the baseline recordings.

2:3 Data Pre-Processing and Analysis

We processed all active task conditions and baseline data with particular attention given to the frontal and temporal leads using Neuroguide analysis software (ver. 2.5.1). All episodic eye blinks, eye movements, teeth clenching, jaw tension, body or neck movements and possible EKG (Electrocardiogram) were removed from the EEG stream. Data were excluded if there was not 60 seconds of usable EEG data for all four conditions. We extracted 4 to 6 seconds of EEG prior to the participant response for each item response in the SPESA condition. Fourier cross-spectral matrices were then computed and averaged over 75% overlapping four-second artifact-free epochs, which resulted in one cross-spectral matrix for each subject and for each discrete frequency. In order to assess the electrophysiological differences within subjects in the experimental conditions we exported the edited EEG data to the Key Institute’s standardized low resolution brain electromagnetic tomography (sLORETA) to localize the generators of the scalp EEG power spectra. The sLORETA solution space is restricted to the cortical gray matter in the digitized Montreal Neurological Institute (MNI) atlas with a total of 6239 voxels at 5 mm spatial resolution [13, 42]. The average common reference is computed prior to the sLORETA estimations. We calculated tomographic sLORETA images corresponding to the estimated neuronal generators of brain activity within each frequency domain [43]. We analyzed the EEG data utilizing the following frequency domains: Delta (0.5 – 3.5 Hz); Theta (3.5 – 7.5 Hz); Alpha 1 (7.5 – 10.0 Hz); Alpha 2 (10.0 – 12.0 Hz) and Beta (12.0 – 32.0 Hz). This procedure resulted in one 3D sLORETA image for each subject for each frequency range. For the sLORETA transformations we utilized spatial – smoothing, signal-to-noise at 1 and linear scaling. We constructed a region of interest file with the MNI coordinates for the 12 seed points for the DNt regions. Each of the ROIs consisted of the current source density from the ROI seed and one single voxel (its nearest neighbor). The resulting file produced log transformed current source density for each seed (ROI). These were organized into spreadsheets and then entered into SAS 9.13 and SPSS 16 for analysis.

In order to test the null model hypothesis and the type III test of fixed effects we utilized a complex linear mixed model with repeated measures. This model sets alpha at .05 using the Tukey adjustment for alternative hypothesis testing. We utilized compound symmetry for the covariance structure, such that observations obtained closer together in time would exhibit higher covariance as compared to observations taken farther apart in time. The mixed model utilized residual a maximum likelihood estimation method, residual variance was calculated via the model profile and the model fixed effects were calculated via the Prasad-Rao-Jeske-Kackard-Harville [44-46] fixed effects method with the Kenward-Roger [47] degrees of freedom method. Least square means (LSM) are in effect, within group means adjusted for the other effects in the model. LSM estimates the marginal means for balanced populations and are also referred to as estimated population marginal means [48]. The type III test of fixed effects utilized in this model assesses the degree of difference between the LSM of conditions. The subjective reports were rated by 3 independent raters. The agreement between raters was assessed using a two-way random effects model with an absolute agreement definition.

2:4 Functional Connectivity

Assessing functional connectivity is typically associated with the degree of correlations (positive or negative) between BOLD levels or CGM between regions in the DNt and which have demonstrated that DNt regions are highly correlated during the resting state [9, 49, 50]. Correlations between regional cerebral glucose metabolism or blood flow and EEG power have been demonstrated, suggesting that EEG power might be associated directly with brain metabolism [51]. However, EEG alpha power fluctuations were not shown to be correlated to the BOLD signal. This lack of association led to the conclusion that it is unlikely that the BOLD activity is directly linked to the neuronal activity responsible for the human EEG alpha rhythm [35]. We assessed functional connectivity with bivariate correlations for the log transformed current source density over multiple EEG segments across subjects, with the hypothesis that specific relationships exist between condition specific regions and Pearson’s product moment correlation coefficient would
adequately reflect the degree of functional integration between DNt regions.

Figure 1: Legend for Functional Connectivity Maps (Appendix I). The numbers in the sLORETA maps are the ROI and the colors in the cortex represent location; the red in the MNI atlas represents the right hemisphere; the blue is midline and the green is left.

III. RESULTS

The following sections show the mixed model results for each frequency domain. The null model likelihood test for all frequencies indicates the model used is significantly more favorable than the null model. The Delta frequency null model likelihood ratio test shows a Chi-square (150.28), 1df, p<.0001. The type 3 test shows significant fixed effects for the conditions F (53.39), df(3), p<.0001 and a significant interaction effect for ROI by Condition with F(6.53), df(44), p<.0001. The Theta frequency null model likelihood ratio test shows a Chi-square (196.09), 1df, p<.0001. The type 3 test shows significant fixed effects for conditions F (46.66), df(3), p<.0001 and a significant effect of ROI by Condition with F(2.56), df(44), p<.0001. The Alpha 1 frequency null model likelihood ratio test shows a Chi-square (159.34), 1df, p<.0001. The type 3 test shows significant fixed effects for conditions F (45.72), df(3), p<.0001 and a significant interaction effect for ROI by Condition with F (2.40), df (44), p<.0001. The Alpha 2 frequency null model likelihood ratio test shows a Chi-square (152.98), 1df, p<.0001. The type 3 test shows significant fixed effects for conditions F (41.75), df(3), p<.0001 and a significant interaction effect for ROI by Condition with F (3.90), df(44), p<.0001. The Beta frequency null model likelihood ratio test shows a Chi-square (167.10), 1df, p<.0001. The type 3 test shows significant fixed effects for conditions F (34.91), df(3), p<.0001 and a significant interaction effect for ROI by Condition with F (4.83), df(44), p<.0001. Figure 2 shows the grand means for log transformed current density levels. It can be seen that the eyes closed baseline (ECB) condition exhibited the greatest amount of current density in the DNt, with decreasing current density as a function of task demand. Table II shows the LSM comparisons for each condition compared to EOB for each frequency domain. The eyes-closed condition shows significantly more activity than eyes-opened in all frequency bands. The SP condition shows significant increases in only the alpha 2 and beta domains. The ES condition shows significant increases in all frequency domains. Table III shows the difference of LSM for between all conditions. In table III from left to right are the condition comparison, estimate, standard error, degrees of freedom, t-value, probability of t and the adjusted probability with the Tukey adjustment. Again the ECB condition shows significantly higher current density levels than all other conditions. The ES condition shows significantly higher levels than EOB in delta, alpha 2 and beta. The SI condition does not show difference from the EOB in the adjusted p values. Significant differences between the SI and ES conditions are shown in the delta frequency only. However, on average the SI shows less current density than ES.

The reliability measures for the subjective experience of the participants during baseline measures show excellent agreement between the three raters. The ECB agreement analysis shows a Chronbach’s Alpha (CA) of .93 with the intraclass correlation coefficient (ICC) of .82 for single measures and .93 for average measures with F (13.97), p = .000. The EOB shows (CA) .95 with an ICC .87 for single measures and .95 for average measures with F (21.28) p = .000. In both the baselines ~89 percent of the reports contained attentional processing and ~11 percent reported attempts to not become bored. The attention to internal state (boredom) could be included in the attention category; however, given the possibility of error we left it coded separately.

Figure 2: Grand mean current density for conditions
Table II: LSM comparisons between conditions. EOB > ECB; EOB > SI and EOB > ES. The comparisons show ECB to be higher in current source density in all frequencies at significant levels. The ES condition shows a similar effect, while the SI condition shows only effects in the alpha 2 frequency, with near significant levels in the beta frequency.

Table III: Differences of LSM for all conditions. In the table from left to right are the condition comparison, estimate, standard error, degrees of freedom, t-value, probability of t and the adjusted probability with the Tukey adjustment.

IV. DISCUSSION

The human brain is perhaps best described as a complex system of complex systems. In essence a reductionist approach to neural functions may hinder the discovery of complex functional systems. Indeed the mechanisms and specificity of its functions are the greatest of enigmas. The DNt continues to be a topic of focused interest and offers promise in increasing our understanding of how the brain orchestrates complex functional processes; including, cognition, affect, self-regulation and memory to name but a few. The current data offer the potential to integrate the EEG with results from other neuroimaging techniques to further our understanding of these complex interactions and their relationship to human behaviors.

This is the first study of its kind to examine the EEG activity in the DNt. The results show similar effects for the overall current density levels as PET and fMRI studies in baselines and active tasks. Our experimental conditions consisted of eyes-opened baseline, eyes-closed baseline, looking at a picture of self and evaluating or match-mismatch.
of self. We will further explore the processing of self as compared to the DNt in a future work. It is, however, suggested that many of the DNt regions are implicated in self-projection, theory of mind and autobiographical self tasks [10, 29, 52, 53]. Furthermore, PET and EEG studies have shown positive correlations of the theta frequency band with CGM in rostral cingulate, and right frontal, middle and temporal gyri with negative correlations in the occipital lobe [54] and positive correlations between CGM metabolism in the thalamus and the alpha frequency in posterior regions [34, 36].

EEG rhythms are proposed to correspond to the synchronized synaptic activity of large numbers of neurons across neural pathways (or networks). The specific functions of EEG oscillatory activity still involve much uncertainty; however, the suggestion that synchronization of distributed neural networks functionally integrates differential brain structures [55] is an important direction for further study. In the following sections we will briefly cover known associations of activations with EEG frequency bands.

In normal populations the delta frequency is most notably associated with the onset of sleep [56] however, it is also suggested to play a particular role in encoding and retrieval as well as having a primary role in overall intelligence measures [57, 58]. The theta frequency is notably associated with memory processes but also in executive attention, in addition to being involved in combination with the gamma frequency in reward motivation [57] the possible governing of cognitive processes [59, 60] and visual encoding and retrieval processes [61-63]. Alpha activity is thought to be involved in all variants of attention, including alerting, orienting and sustained attention, as well as visual processing and cognitive preparedness [30, 31, 64-66]. Additionally, alpha is shown to play a role in evaluation of self and mental state decoding [41, 67]. Beta activity is proposed to be involved in affective and cognitive processes, attention as well as executive functions and psychopathology [68-70].

The functional connectivity (FC) maps in Appendix I, first and foremost reflect the possible integration of functional task specific neural networks. The ECB and EOB conditions appear similar in FC with the ECB showing greater involvement of regions and specific connectivity between right parietal and right frontal regions that are not shown in EOB. Similarly, the left parietal region shows connectivity with more frontal locations during ECB than EOB. The SI condition shows less connectivity which may be indicative of functional specificity involving posterior midline and left parietal to left prefrontal regions and contralateral prefrontal interactions. The ES condition is of particular note concerning the right somatosensory region. This area appears highly functionally integrated with left frontal and midline regions. The theta frequency shows the same overall effect for ECB to EOB; however, the right parietal area shows more FC with anterior left and midline regions. This possibly reflects allocation of muscle-regulatory-memory-knowledge since the right parietal lobe plays a role in attention, orienting and spatial processing. The SI condition also shows specific FC between right parietal and left prefrontal regions, as well as FC between most frontal regions with the exception of bilateral frontal integration. The ES does not involve the right parietal region in the theta band; however, FC between left parietal and left frontal regions appears more specific. This is possibly attributed to the language processing and verbal response selection components of this task or an integration of memory, language, attention and affect. The alpha 1 frequency shows differential effects for ECB and EOB with similar FC for right parietal to frontal; however, different FC for posterior cingulate to frontal and left parietal to frontal. The SI condition shows specific FC from posterior cingulate to right frontal and left dorsolateral prefrontal regions and right parietal to the DLPFC and lateral PFC and the ES condition shows an apparent concentration of FC between left posterior regions and left prefrontal and midline structures. The Alpha 2 and beta frequencies show a bilateral parietal interaction in EOB as contrasted with ECB. More interestingly specific FC effects are shown for the left parietal and right prefrontal in alpha 2 during ECB but not in EOB; contrarily, this is reversed in the beta frequency. The SI condition shows specificity in FC between PC and left frontal. Also right parietal with right frontal, midline and left prefrontal regions, while beta activity appears to increase FC between bilateral parietal regions and between right parietal and right prefrontal. The ES shows a high degree of FC between PC and medial prefrontal regions. Additionally, left parietal regions show FC patterns with the right prefrontal cortex. Similarly, the beta frequency shows FC toward the right and midline from left parietal areas, while the posterior cingulate shows specific FC with the anterior cingulate, ventromedial PFC and left temporal cortex.

V. CONCLUSIONS

The activity in ECB and EOB are very similar to studies examining functional connectivity in executive attention [30, 71, 72] and suggest, in combination with the subjective reports of this study, that attentional processing may best reflect the “what” of the default mode. The SI and ES conditions involve regions shown active during self-image recognition, self-referential processing and autobiographical memory which suggest that many of the DNt regions do play a role in self-referential processing. Further study of the EEG in the DNt is warranted and may increase our understanding of how neural pathways communicate and integrate to functionally influence human behavior.

APPENDIX

I: SLORETA FUNCTIONAL CONNECTIVITY MAPS

ACKNOWLEDGMENT

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also like to express appreciation to Deymed Diagnostics for the use of their Truscan EEG Acquisition system.

REFERENCES


APPENDIX

I: Bivariate correlations between the DNt regions during each task condition. From top to bottom are the frequency domains and from left to right are the conditions. The images are horizontal slices with notation for left and right in the top of the frame. The green in the images are rois in the left hemisphere, the red are in the right and the blue are medial/middle. Only significant correlations are shown in the images. Each color represents the specific ROI’s functional connectivity with other DNt regions.

<table>
<thead>
<tr>
<th>Frequency</th>
<th>ECB</th>
<th>EOB</th>
<th>SI</th>
<th>ES</th>
</tr>
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<tr>
<td>Delta</td>
<td><img src="#" alt="Image 1" /></td>
<td><img src="#" alt="Image 2" /></td>
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<tr>
<td>Theta</td>
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<td><img src="#" alt="Image 6" /></td>
<td><img src="#" alt="Image 7" /></td>
<td><img src="#" alt="Image 8" /></td>
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<td>Alpha 2</td>
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