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The Brain Time Toolbox, a software library to retune electrophysiology data to brain dynamics

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Abstract

Human thought is highly flexible, achieved by evolving patterns of brain activity across groups of cells. Neuroscience aims to understand cognition in the brain by analysing these intricate patterns. We argue this goal is impeded by the time format of our data – clock time. The brain is a system with its own dynamics and regime of time, with no intrinsic concern for the human-invented second. Here, we present the Brain Time Toolbox, a software library that retunes electrophysiology data in line with oscillations that orchestrate neural patterns of cognition. These oscillations continually slow down, speed up, and undergo abrupt changes, introducing a disharmony between the brain's internal regime and clock time. The toolbox overcomes this disharmony by warping the data to the dynamics of coordinating oscillations, setting oscillatory cycles as the data's new time axis. This enables the study of neural patterns as they unfold in the brain, aiding neuroscientific inquiry into dynamic cognition. In support of this, we demonstrate that the toolbox can reveal results that are absent in a default clock time format.

Studying dynamic cognition

Everyday tasks involve a plethora of cognitive functions that operate dynamically in tandem. Something as mundane as taking notes during a meeting or battling your friend in a video game requires attention, motor activity, perception, memory, and decision-making, each evolving over time. How does the brain achieve dynamic cognition? To answer this question, neuroscientists closely study how brain activity unfolds from one moment to the next using temporally precise neuroimaging methods. These include electroencephalography (EEG), magnetoencephalography (MEG), and single and multi-unit recordings – grouped together under the term electrophysiology.

Seconds are foreign to the brain

In a typical electrophysiology study, neuroscientists first probe cognition by introducing an experimental manipulation. For example, an attention researcher might introduce a set of moving dots. Then, to understand cognition in the brain, they perform a series of analyses on the recorded data. They might study changes in scalp topography over a second of data, apply machine learning to characterize how the representation of the dots evolves, or perform any other time-dependent analysis.

Critically, from the raw output of neuroimaging devices to the analysis of recorded brain signals, time is operationalized as clock time – sequences of milliseconds. We claim that clock time, with all its benefits for human affairs, is generally inappropriate for neuroscience. This is because clock time is defined by us and for us, based on how long it takes for Earth to rotate its axis. The brain itself, however, employs its own regime of time, dictated by its own dynamics. As such, the brain is indifferent to how many milliseconds, seconds, minutes, or hours have passed unless it is expressly relevant for specific behaviour, such as maintaining circadian rhythms [1] or tracking a time-dependent reward [2]. Instead, the brain is concerned with coordinating communication between cells in a delicate time-sensitive manner, such as sending information at one moment and receiving feedback signals at the next. Hence, the brain's intrinsic time format – brain time – is dictated by the internal processes that clock brain activity (for an explanation of key terms, see the Glossary in Table 1).

Cycles as the brain's native unit

How is brain activity organized? A defining feature of the brain is that its activity waxes and wanes [3], pointing to a central role of brain oscillations. Brain oscillations are well-gearred to structure brain activity. For one, each cycle of an oscillation contains a window of excitability where cells are more likely to fire [4,5]. Moreover, oscillations vary in their frequency, meaning the excitability windows vary in duration. The functional role of oscillations has been shown across a wide array of cognitive functions, including attention [6,7,8], perception (auditory [9,10], visual [11,12], tactile [13,14]), action [15,16], memory [17,18,19], and decision-making [20,21]. Together, this situates brain oscillations as the brain's clocking mechanism, clustering brain activity in flexible ways to organize dynamic cognition. The brain's base unit of time then, are the cycles of oscillations that coordinate neural firing, not the milliseconds with which we format our data.

Clock and brain time are usually out of tune

Why does it matter that we use a foreign time format? When neuroscientists study dynamic cognition, they repeat measurements across trials, resetting their stopwatch at the start of each. However, some oscillations do not reset [22,23]. Even when most do, oscillations evolve continuously in frequency and show jumps in phase (Figure 1). Thus, besides a potential mismatch between clock and brain time from the get-go caused

by variable starting phases, the disharmony between the dimensions accumulates due to frequency drift and phase jumps. These are prime examples of eccentricities in brain dynamics, formally called non-stationarities (and there are more [24]). Their presence makes clock time an ill-suited format to study temporal patterns of dynamic cognitive function – it distorts how the brain itself carries information forward in time.

To demonstrate this point, take again the case of spatial attention. Studies show that alpha oscillations (8 to 12 Hertz; Hz) in parietal regions orchestrate the dynamics of spatial attention [25,8]. If these oscillations vary in their starting phase across trials, then the neural patterns of spatial attention will vary along with it. Likewise, if the oscillations slow down in frequency, the patterns slow down too. If a researcher is interested in, say, decoding the locus of covert attention in the visual field over time, it would muddy the waters to do so in clock time, ticking away with its equal periods. The slowing down of alpha oscillations means brain time falls behind relative to clock time, so analysing the data in its default format yields a sped-up readout of attention's true pattern. Instead, we argue the dynamics of clocking oscillations should heavily inform data analysis. As a general mantra, the optimal approach to analyse the brain, like any other system, is with recourse to its own dynamics – from inside out [26,27] (Figure 2).

The problem of disharmony does not end here. Neuroscientists repeat measurements across participants to establish whether effects found in the data are representative and statistically robust. But different brains have different dynamics, resulting in disharmony *across* brains too. In the attention experiment, it is highly relevant that the clocking alpha oscillations differ in frequency from person to person [29] as it means the patterns differ too. Looking for evolving patterns of spatial attention by averaging across participants is like asking when spring turns summer in a solar system that contains diverse planets – it only makes sense after correcting for individual dynamics (Figure 2).

Approaches to factor in brain time

Disharmony between clock and brain time impedes scientific analysis within and across brains. To overcome this problem, approaches have been developed that factor in brain dynamics. At minimum, the phase of oscillations can be tracked to explain some of the variance in brain data [19] or behaviour [30,31], and analyses can be locked selectively to oscillatory peaks or troughs [32]. Then there are more expansive techniques, where the electrophysiological data is restructured before any analysis is carried out. These include organizing the data with phase as the time axis [33], as well as linear time warping approaches that transform a template signal based on trial-by-trial variations in brain dynamics [34].

Such approaches can reveal brain patterns of interest that are otherwise obstructed by clock time's distorting effects. For example, the phenomenon of phase precession has been extended from rodents to humans when using phase as the time axis, with no such effect visible in clock time [33]. As another example, linear time warping uncovers oscillatory brain patterns on the trial average by correcting for differences in brain time across trials [34].

While these approaches come a long way in factoring in brain dynamics, each is limited in their scope. Using phase to explain variance in the data or locking analyses to peaks or troughs provides insights about selective data samples but does little to enable the readout of dynamic patterns. Setting the time axis to phase may not always be possible and departs significantly from the original data structure – such that unique phase-based analyses are needed. Linear time warping can

equalize brain time across trials but is less equipped to deal with non-stationarities throughout the trial due to its linear nature.

A dynamic and holistic way to factor in brain time

Here, we introduce **brain time warping** as a method to account for the disharmony between clock and brain time. This approach overcomes previous limitations in the following way. First, it identifies segments throughout each trial where clock and brain time fall out of tune. Then, it adapts the data to reduce their difference – winding back clock to brain time sample by sample (Figure 3). Brain time warping incorporates an algorithm called dynamic time warping (DTW), which characterizes the similarity of two signals [35,36]. DTW computes a warping path, which shows how the samples of each signal need to be transformed to optimize their alignment. For brain time warping, those signals are clock and brain time (Figure 3A).

How are clock and brain time operationalized? Brain time can be characterized as the phase of the oscillations hypothesized to orchestrate a process' dynamics, with its variable starts, drift, and phase jumps. Clock time can be characterized as the phase of a stationary sine wave, fluctuating away faithfully to seconds. Such a signal is what brain time would look like without the three sources of disharmony; here milliseconds and cycles map directly onto each other. (For example, in Figure 3A, multiples of 100 milliseconds correspond to each zero-crossing of the clock time signal.)

DTW highlights during which samples clock and brain time fall into disharmony, and this warping path can be used to transform the original data. Concretely, at samples where the warping path suggests brain time needs to repeat itself before ramping back up to clock time, brain time warping repeats samples in the original data (Figure 3C). Looping back to our attention example, at segments where DTW indicates alpha oscillations slow down, brain time warping stretches the data by repeating samples in an attempt to bring its structure closer to the true dynamics of spatial attention.

Brain time warping loops over trials, continuously correcting disharmony by applying the warping path cycle by cycle. In effect, brain time warping adapts data to the dynamics of an oscillation of interest in a data-driven way. The result is a dataset in brain time rather than clock time, and as such, the time axis has changed from seconds to cycles. As the data is referenced to individual dynamics, it also becomes easier to look for temporal patterns across brains. Here, we introduce the **Brain Time Toolbox** (https://github.com/sandervanbree/brain_time_toolbox, Supplementary Methods), a toolbox built for MATLAB (The MathWorks, Natick, Massachusetts, USA) that implements brain time warping and tests its effect. This software library was built for electrophysiology data analysis, including EEG, MEG, and single and multi-unit recordings. The toolbox lets users select a brain time signal from one or more warping sources (e.g., channels or independent components extracted from a data structure; Supplementary Methods, Toolbox, section 2.2.1). This signal then serves as the basis for brain time warping as laid out in Figure 3. In the upcoming section, we methodologically validate brain time warping – utilizing the toolbox throughout.

Results

We tested the algorithm's effects across three electrophysiology datasets. In the first dataset (N = 10 participants), we simulated a basic attentional spotlight model, giving us full control over the ground truth brain patterns (Figure 4A). Briefly, we placed one conducting dipole in the right parietal cortex, which exerted top-down control over the phase of two follower dipoles, one located in each visual cortex. We generated two conditions, one

where attention was oriented to the left hemifield, and one to the right. These conditions systematically differed in their underlying brain activity. Specifically, the conducting dipole always forced its contralateral follower to the same phase while setting an anti-phase relation with its ipsilateral follower (drawing upon experimental findings [37,38,39]). In addition, the conducting dipole inhibited the contralateral follower dipole, reducing its amplitude [40]. We then injected the data with variable starting phases and frequency drift to mimic natural brain activity.

In a second dataset (N = 7 sessions), we warped intracranial data from rodents navigating through a square field (Figure 4B; data obtained from [41]). Here, we were interested in characterizing the dynamics of the local field potential (LFP) and grid cell firing patterns in the entorhinal cortex. Just like in the simulation, we again formatted the data into two conditions. Specifically, the data was split based on whether the animal was travelling through a field coded by the grid cell or through another location not coded by the grid cell.

In a third dataset (N = 16 participants), we warped EEG data recorded while human participants observed moving dots (Figure 4C; data obtained from [42]). The two conditions were set around the motion direction of dots – with one condition comprising trials with leftward motion, and the other comprising rightward motion. In Supplementary Methods (Datasets, section 1), we report additional details on each dataset.

Basic analyses

In basic analyses, we asked whether warping recovers oscillatory neural activity for each dataset by comparing clock and brain time on a number of measures. For these analyses, we pooled across conditions – focusing on general effects of brain time warping on electrophysiology data and ignoring cognition for the moment. First, we tested whether warping increases the oscillatory structure of event-related potentials of channels near the predicted location of coordinating brain oscillations. This analysis provides a qualitative indication on the question of whether brain time warping overcomes non-stationarities.

Second, we performed a time frequency analysis across all channels and tested whether warped data reveal a higher peak at the predicted frequency of interest in the power spectrum. This quantifies the degree to which brain time warping is able to overcome frequency drift and phase jumps in the data.

Third, we compared the intertrial coherence (ITC) across all channels between clock and brain time. This measure tests for the consistency of oscillatory phase across trials and thereby additionally taps into the degree to which the algorithm overcomes variable starting phases (which ordinarily reduce ITC by jittering the phase relation across trials). We predicted that brain time warping increases ITC at the predicted frequency of interest by equalizing brain time across trials.

Brain time warping recovers oscillatory activity

In the simulated dataset, the event-related average of clock time data shows no robust oscillatory shape. After warping, the oscillatory structure hidden in the data becomes qualitatively uncovered (Figure 5A). Moreover, we found that the algorithm sharpens the power spectrum selectively around the warping frequency (Figure 5B), and, in line with our hypothesis, increases the peak's magnitude. Third, the ITC in clock time shows comparatively low values around simulated alpha rates – with only weak clustering at low alpha (Figure 5C). ITC is enhanced by brain time warping, revealing a strong cluster at participants' warping frequency. We find similar results for the rodent dataset (Supplementary Results, section 3.2.1). For the

human data, we found a prominent increase in ITC at the warping frequency, but not in the peaks of the power spectrum (Supplementary Results, section 3.3.1). Together, these results demonstrate that warping can reveal oscillatory activity that is lost due to clock time's distorting effects on the data.

Advanced analyses

In advanced analyses, we tested whether brain time warping unveils dynamic patterns of cognition. For each dataset, the conditions were set up such that their contrast was expected to yield a difference in brain activity that makes for a neural signature of cognition. For example, in the human dataset, the difference in neural activity between leftward and rightward motion trials estimates the neural signature of spatial attention because activity unrelated to attending to one or other spatial direction is factored out. If oscillations of interest dynamically clock the neural processes underlying cognition, this should cause the neural signature to vary along with the oscillations.

Pattern classifiers capitalize on neural signatures to make predictions about condition (i.e., class) membership of untrained data. As such, classifier performance makes for a useful index of the fidelity of neural signatures of cognition – with fluctuations of classifier performance indicating fluctuations in the neural signature (periodicity; [43]). Building off these assumptions, we predicted that brain time warping enhances periodicity of these neural signatures by adapting for non-stationarities in the data.

To test this, we used a linear discriminant analysis (LDA) to classify condition in each dataset. We trained the LDA on each timepoint and tested how well it generalized to all other timepoints [44]. This resulted in a two-dimensional temporal generalization matrix (TGM) that provides a robust map of classification performance over time (and so too of the fidelity of the neural signature). In summary, we assumed periodicity in TGMs is a high-level measure to detect periodic brain patterns of cognition, and we predicted that brain time warping would increase such patterns by factoring in the dynamics of clocking oscillations.

Quantifying periodicity

For the advanced analyses, we quantified TGM periodicity by applying a Fast Fourier Transform (FFT) over each row and column of TGMs. Then, we averaged the resulting spectra into a single spectrum – the *periodicity spectrum*. This spectrum quantifies how much the neural signature fluctuates at different frequencies. To test our hypothesis that brain time warping increases the oscillatory structure of neural signatures, we contrasted the spectra obtained from clock and brain time data against each other – comparing the periodicity at predicted frequencies of interest.

Moreover, to aid visual inspection of periodicity, we also report autocorrelation maps of TGMs for each dataset. These maps are generated by correlating TGMs with iteratively shifted versions of itself, resulting in a representation of its self-similarity that brings out latent periodic structure [45].

Statistically testing periodicity

To evaluate which frequencies in the periodicity spectrum are statistically reliable, we compared the empirically derived spectrum with periodicity spectra obtained under the null hypothesis that there is no fluctuating neural signature of cognition. To do so, we created a pool of TGMs obtained from an LDA trained using randomly permuted classification labels. This procedure destroys the true class structure inherent to the data [46], leaving the classifier with pseudo neural signatures that do not contain generalizable information about the cognitive process under investigation. To establish statistical

reliability, we compared the magnitude of peaks in empirically derived TGMs with the distribution of magnitudes in TGMs obtained with permuted labels – both for clock time and brain time data. For more details on basic and advanced analyses, see Supplementary Methods (section 1.1.1 and 1.1.2).

Brain time warping recovers neural patterns of cognition

In the simulation, the neural signature provided by the classes reflected attention. The simulated patterns of this signature were not detectable in a default clock time format but did emerge after brain time warping (Figure 6).

In the rodent data, the difference in activity between classes reflected whether the animal was in a place field coded by grid cells, yielding a signature of the neural basis for spatial navigation [49]. In clock time, no periodicity is evident over time (Figure 7A; top) despite grid cells strongly phase locking to theta oscillations ([50]; Supplementary Results, section 3.2.3). Importantly, brain time warping the firing rates of grid cells to theta oscillations obtained from the LFP does result in periodicity (Figure 7A; bottom).

In the human data, the neural signature reflected spatial attention, provided by the difference in brain activity to left- and rightward motion. While the clock time data qualitatively shows some periodicity at alpha, the peaks do not stand out reliably from the peaks in periodicity spectra obtained with permuted labels (Figure 7B; top). In contrast, brain time warping reveals prominent and reliable periodicity at participants' individual alpha frequency (Figure 7B; bottom). Together, the basic and advanced results indicate that brain time warping is a promising tool to repair disharmony between clock and brain time, facilitating the study of the dynamic cognitive brain.

Discussion

Is retuning using brain time warping circular?

A potential concern with brain time warping could be that it trivially imposes oscillatory structure onto the data. The worry here is that the algorithm makes data patterns fluctuate at the warped frequency no matter which frequency is selected. In this section we argue when the algorithm is on safe grounds, and when vigilance is needed.

First, as a note of clarification, the path used for brain time warping does not contain oscillatory structure. That is to say, if the path were applied to a random time series, it would not mould it to increase its oscillatory shape. This is because the path is instead designed to show when the oscillation used for warping undergoes non-stationary behaviour. Nevertheless, an important concern remains. Brain time warping applies the path to the data in order to align it with brain dynamics, so if the warping signal is within the data, its stationarity will increase – introducing some oscillatory structure after all. Whether circularity is a problem depends on two factors: the type of analysis carried out, and the dependence between warping signal and warped data. We discuss these points in turn, first covering each type of analysis.

Basic analyses

Brain time warping is expected to enhance oscillatory structure in the ERP, power spectrum, and ITC at least somewhat because there are usually at least some oscillations at any frequency to begin with. So, warping to a random frequency will cause those oscillations to have their non-stationarities reduced, affecting subsequent results. Hence, any increase around warping frequencies in basic analyses should not be taken as evidence that those frequencies are critical for cognition – there needs to be a further relation to independent measures (such as cognitive or orthogonal neural variables). In this sense, brain time warping can be used as a pre-processing step to aid subsequent

high-level approaches that are sufficiently independent (to avoid circular inference [51]).

With that said, we find that warping to weak simulated oscillations results in only weak frequency-specific enhancements compared to warping to strong oscillations – speaking to the specificity of brain time warping even before cognition enters the scene ([Supplementary Methods, section 1.2.2](#)).

Advanced analyses

We have presented the advanced classification analysis as a circularity-free high-level approach – and it is the central analysis implemented in the Brain Time Toolbox. By tapping into neural signatures of cognition rather than oscillations themselves, warping-induced changes are nontrivial. Specifically, only warping to those oscillations which coordinate the underlying activity relevant for cognition is expected to yield fluctuations in cognition’s neural signature. In support of this, we performed a control analysis where we warp to control frequencies [52], resulting in no evidence of periodicity ([Supplementary Methods, section 1.2.2](#)). A further safeguard of the advanced analysis is that the obtained null distributions benefit equally from any trivially imposed oscillatory structure as the empirical distribution.

Data dependence

Beyond the type of analysis that is used, the dependence between warping source and transformed data is another factor to consider. After all, if the cause for circularity lies chiefly in changes to the warping signal, then removing it from the warped data reduces circularity concerns. We report suggestions on how to achieve data independence for each electrophysiology method, describing how they can be implemented before or after warping ([Supplementary Methods, Toolbox, section 2.4.1](#)). We also report cases in which independence between warping source and data is impossible. Here, it is important to determine on a case-by-case basis whether circularity is a concern based on the previous points (i.e., are subsequent analyses orthogonal or not?). To aid this process, the toolbox tracks dependence between warping source and warped data and raises a warning when circularity could become an issue.

Statistical false positives

With these reflections in mind, we finally emphasize that brain time warping is a hypothesis-driven method that capitalizes on the temporally coordinating nature of oscillations. Hence, we recommend warping only using oscillations predicted to fit that bill to avoid false positive results by chance, or to apply multiple testing correction when re-warping to a different signal in the data. To enable hypothesis-driven warping, the Brain Time Toolbox computes a variety of information about warping signals – including their time frequency characteristics, waveshape, and topographical profile – allowing users to make informed decisions about which signal they wish to designate as brain time.

When is retuning clock and brain time necessary?

The need to use brain time warping or other methods to retune depends on (1) the degree to which clock and brain time are in disharmony, and (2) the degree to which such disharmony interferes with analyses. Below, we elaborate on both criteria.

The degree to which disharmony is present depends on the levels of processing involved in the employed experimental paradigm. Take once again the spatial attention study. Between the moving dots’ light hitting the participant’s retina and their pressing of the button to indicate motion direction, a vast amount of subcortical and cortical processing transpires. While

internal dynamics start to coordinate stimulus processing as early as the thalamus [53,54], or even earlier [55], disharmony is most prevalent in higher level regions – where processes such as attention and decision-making operate in full swing. This is because at this late stage, information has passed through many cell ensembles where different oscillations have each exerted a temporal footprint. As these footprints add up, clock time falls increasingly out of tune with brain time. As a result, we lose track of brain dynamics and the information they provide about cognition, such as whether dots make it to awareness [56] or whether features of the dots (such as their colour) are available to working memory [57]. Thus, there is a gradation in clock time’s distorting effect which depends on the extent of cortical processing. Research that restricts analyses to low-level subcortical processing or very early evoked potentials benefits comparatively little from retuning, while retuning may be a vital step to understand brain patterns in late stages – with at least one exception: retuning is unnecessary for analyses that do not rely on temporal variations of the neural signature. For example, a researcher may want to study the trial-average activity in parietal regions as a function of the proportion of dots that moved, or map aggregate differences in network connectivity between participants. Here it is true as ever that brain dynamics play their part in the subprocesses involved, but the analyses are insensitive to time variations, leaving them unaffected by oscillations’ footprint.

In short, retuning clock and brain time is necessary depending on the degree to which both the mechanisms of study and the employed analyses depend on the brain’s internal dynamics. On the whole, few electrophysiology studies are exempt from clock time’s distorting effects.

Brain time is not unitary

The phrase “brain time” is used to emphasize the conceptual departure from a format extrinsic to the brain. We do not mean to suggest that there is a single brain time. Rather, different cognitive processes are clocked by different groups of oscillations, each with their own frequency and source. In this sense, brain time is analogous to a concept like “Earth time”, which contrasts itself with time on other planets whilst further decomposing into different time zones. Finally, brain time in the present context does not refer to *timekeeping* in the brain. Instead, it refers to the oscillatory dynamics by which the brain coordinates cognition generally, of which temporal cognition is a specific instance [58].

Conclusion

Where does this leave us? We believe that rather than imposing a foreign unit of time onto the brain while studying its function, the brain is best understood as a system with its own dynamics and temporal organization. Upon inspection, the brain operates rhythmically, with brain oscillations as a key player. This has important consequences for scientific analysis. If it is true that oscillations clock brain activity to coordinate cognition, then their dynamics should heavily inform how we study evolving data patterns. In contrast, analysing such patterns in the default clock time format is likely to yield a distorted readout as the brain’s internal dynamics do not scale linearly to sequences of (milli)seconds. We introduce brain time warping as a method to account for disharmony in brain data, dynamically transforming electrophysiology data structures in a way that brings them in line with brain dynamics. The Brain Time Toolbox implements brain time warping, facilitating analysis on the oscillatory dynamics of the cognitive brain.

Data availability

We re-structured and re-analysed the data of [41], and simulated new data, which are available in the Brain Time Toolbox at <https://github.com/sandervanbree/braintime>. We re-analysed the data of [42], which is available at <https://osf.io/bpexa/>.

Code availability

Code for the brain time analysis of the rodent and simulated data is included in the Brain Time Toolbox at <https://github.com/sandervanbree/braintime>. Custom code for analysis of the human data is available from the corresponding author upon request.

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Author Contributions

The Brain Time Toolbox was conceived and developed by S.B., M.M. & S.H., with consultation from L.K., C.K., & M.W. The simulated dataset was generated and analysed by S.B., M.M. & S.H. The remaining datasets were analysed by S.B. & S.H. The manuscript was written by S.B. & S.H. with input from M.M., L.K., C.K., & M.W.

Competing Interests

The authors declare no competing interests.

Figure Legends/Captions

Figure 1: Sources of disharmony between clock and brain time

Brain oscillations are non-stationary, which causes a non-correspondence or “disharmony” between the brain’s internal dynamics and clock time. (A) An oscillation shows frequency drift and a spontaneous jump in phase, resetting itself. (B) Two oscillations with different starting phases. The blue oscillation starts with a rising phase, while the sand-coloured oscillation starts with a falling phase. The top rows of each panel show the amplitude fluctuations of oscillations, while the bottom rows show the phase.

Figure 2: What is the best way to study a foreign system?

(Left) Imagine a planet with seasonal dynamics radically different from Earth’s, where the duration of each season differs substantially (as a real-world example, planet Kepler-413b has erratic seasons due to its eccentric orbit [28]). To understand the system, we measure a variable of interest across time, such as surface temperature. Critically, how do we define time here? If we plot temperature as a function of Earth’s seasons (Earth time), the data will be heavily distorted, hampering interpretation. Instead, if we were to study the system with recourse to its own dynamics (system time), the same temporal patterns in the data become interpretable.

(Right) As neuroscientists, we are in an analogous position – we are studying a foreign system with its own dynamics. So, in the same vein, we should interpret data patterns with reference to the brain’s dynamics, enabling an accurate readout of evolving patterns of information.

Figure 3: Brain time warping between clock and brain time

(A) Brain time starts in its rising phase and slows down its frequency over the course of the trial, both causing a mismatch to clock time (defined as a stationary signal fluctuating in sync with a researcher’s stopwatch). (B) To facilitate warping, the phase of clock and brain time are unwrapped, meaning phase is computed without cycle resets. (C) DTW calculates a warping path that minimizes the difference between the dimensions. Cycle by cycle, the path is applied to the input electrophysiology data, transforming its dynamics in accordance with the brain’s dynamics. To enable alignment of brain time across trials, the data of each cycle is resized to a constant number of samples. The previous steps are repeated for all remaining trials. Upon completion, the data’s time axis is changed from seconds to cycles of brain time. The data is no longer in clock time, but in brain time.

Figure 4: Electrophysiology datasets used to validate brain time warping

(A) Simulated electroencephalography (EEG) data (N = 10 virtual participants). We developed a basic attentional spotlight model with dipoles oscillating at alpha frequencies (8 to 12 Hertz [Hz]). One parietal conductor dipole controlled two follower dipoles, one in each visual cortex. Two conditions differed in brain activity due to the phase relation across dipoles and the suppressed amplitude of the contralateral follower dipole, together yielding attention’s neural signature. To introduce disharmony between clock and brain time, we added frequency drift and variable starting phases to the data. We brain time warped to alpha oscillations in visual regions (right). (B) Rodent single and multi-unit data (N = 7 sessions). Long-Evans rats navigated through a square field while single units and local field potentials (LFP) were recorded from the entorhinal cortex. We identified grid cells and cut the data depending on whether the animal was traveling through a location coded by a grid cell (condition 1) or not (condition 2). We display cell spike locations in the field, its smoothed representation (rate map), and this representation’s autocorrelation. We then brain time warped grid cell firing patterns to theta oscillations (4 to 8 Hz) measured in LFP recordings (bottom right). (C) Human EEG data (N = 16 participants). Participants viewed random dot kinematograms, with dots moving at one of two levels of coherence (25.6% or 51.2%) in a direction ranging from 1° to 360°. We pooled the levels of coherence and binarized direction toward left- (condition 1) or rightward (condition 2) motion. We then brain time warped the EEG data to parietal alpha oscillations (bottom right).

Figure 5: Results of basic analyses in the simulated dataset

(A) Event related potentials (ERPs) in the left visual cortex of one example virtual participant. In clock time, averaging across trials destroys the simulated oscillatory structure. By repairing disharmony, brain time warping recovers this structure. (B) Power spectra averaged across all channels and participants. Brain time warping increases the power of alpha oscillations at the simulated rate for each participant. Brain time results are always re-referenced to individual participants’ brain time rate ($\frac{\text{clock time frequency}}{\text{warping frequency}}$). This sets 1 Hz as each participant’s warping frequency (and e.g., 0.5 Hz as half the warping frequency). We removed the aperiodic (1/f) component of the power spectrum using the FOOOF toolbox [47]. (C) Intertrial coherence (ITC) averaged across all channels and participants. Brain time warping increases ITC at the (ground truth) alpha frequency. The analysis window was restricted to 1 to 2 seconds to reduce artefacts. We equalized the y-axis in (B) and the colour axis in (C) between clock and brain time based on maximum values to enable a visual comparison between dimensions (this step is performed in all figures).

Figure 6: Results of advanced analyses in the simulated dataset

We tested for periodic patterns in the classifier’s temporal generalization matrix (TGM), which provides an index of neural signatures of cognition by demonstrating how the classifier’s performance generalizes across time. (A) An example participant’s TGM shows no periodic structure in clock time (top). After brain time warping, the simulated periodic structure in the neural signature is recovered – as evidenced by the checkerboard pattern (bottom). (B) The difference between clock and brain time becomes qualitatively striking in the TGM’s autocorrelation maps. (C) We quantified periodicity by applying a fast Fourier transform over all rows and columns of TGMs. Then, we perform second-level statistics by comparing empirical periodicity with permuted periodicity (obtained by shuffling class labels). Only brain time spectra show significant periodicity at the warping frequency ($p < 0.001$) and its first harmonic ($p < 0.05$), demonstrating brain time warping corrects for disharmony and unveils ground truth neural signature dynamics (bottom and top). Each participant showed periodicity peaks selectively at their warping frequency. We corrected for multiple comparisons (using false discovery rate; FDR [48]), except at specific frequencies in the brain time spectra at which we hypothesized classifier periodicity (0.5 Hz, 1 Hz, 2 Hz; 1 Hz remains significant when applying FDR). **In Supplementary Methods, we report the full methods (section 1.2). In Supplementary Results, we provide additional plots, including all TGMs, autocorrelation maps, and periodicity spectra (section 3.1).**

Figure 7: Results of advanced analyses in the rodent and human dataset

(A) Warping the rodent data to LFP theta unveils statistically robust periodicity around the warping frequency and its first harmonic ($p < 0.001$), while the clock time spectrum shows no significant peaks. (B) In the human dataset, brain time warping reveals periodic patterns around the warping frequency ($p < 0.001$), indicating the neural signature of attention fluctuates during motion perception. For the rodent data, each session showed periodicity peaks selectively at their warping frequency. For the human data, not all participants showed periodicity peaks, and there was some variance in the brain time frequency of peaks. The insets display autocorrelation maps of TGMs from example sessions (for the rodent dataset) or example participants (for the human dataset). **In Supplementary Methods we report the full methods (section 1.3 and 1.4). In Supplementary Results, we provide additional plots (section 3.2 and 3.3). These**

plots include TGMs, autocorrelation maps, periodicity spectra, grid cell maps, and spike-field coupling between theta and single unit spikes

Table 1: Glossary

Term	Description
Anti-phase	Two oscillations are in anti-phase when they stand in opposite relation to each other – for example when the peak in one oscillation co-occurs with the other's trough
Brain oscillations	Rhythmic fluctuations of brain activity generated by populations of cells
Brain time	Time as sequences of cycles of a coordinating brain oscillation
Brain time warping	Algorithm that employs dynamic time warping to transform electrophysiology data in accordance with brain time dynamics
Brain time toolbox	Software library that implements brain time warping and tests its effects
Clock time	Time as sequences of seconds
Dynamic time warping (DTW)	Algorithm that can measure the similarity between signals and minimize their difference
Frequency	Number of cycles per time window (typically a second)
Linear Discriminant Analysis (LDA)	Machine learning method that maximizes the separability between two classes of data by applying linear transformations to it
Local Field Potential (LFP)	The electric potential recorded from extracellular space around cells
Neural signature	Brain activity that systematically correlates with, in the present context, a cognitive process
Non-stationarity	A signal is non-stationary when it undergoes spectral changes over time. We focus on frequency drift, variable starting phases, and phase jumps
Periodicity	Fluctuating patterns of a neural signature
Phase	Metric to indicate the specific point in the cycle of an oscillation. Two oscillations are in phase when (for example) their peaks align
Phase precession	Phenomenon where place cells fire at progressively earlier phases of theta oscillations as an animal moves across a trajectory
Temporal Generalization Matrix (TGM)	Representation of how a classifier trained to separate classes of data on one timepoint performs on other timepoints. When a classifier generalizes, it indicates the neural signature remains stable
Warping path	Representation of how two signals need to be resampled to minimize their difference
Warping source	Data structure containing potential coordinating brain oscillations used for brain time warping

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