Intrinsic neural timescales – Temporal integration and segregation

Authors:

Annemarie Wolff[1*], Nareg Berberian[1*], Mehrshad Golesorkhi[1], Javier Gomez-Pilar[2,3], Federico Zilio[4], Georg Northoff[1,5,6]

1. Mind, Brain Imaging and Neuroethics Research Unit, Institute of Mental Health Research, The Royal Ottawa Mental Health Centre and University of Ottawa, Ottawa, Canada
2. Biomedical Engineering Group, University of Valladolid, Paseo de Belén, 15, 47011 Valladolid, Spain
3. Centro de Investigación Biomédica en Red en Bioingeniería, Biomateriales y Nanomedicia, (CIBER-BBN), Madrid, Spain
4. Department of Philosophy, Sociology, Education and Applied Psychology, University of Padova, Padua, Italy
5. Centre for Cognition and Brain Disorders, Hangzhou Normal University, Hangzhou, China.
6. Mental Health Centre, Zhejiang University School of Medicine, Hangzhou, Zhejiang, China.

* Equally contributing first authors

Correspondence: georg.northoff@theroyal.ca (Georg Northoff)

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Abstract:

We are continuously bombarded by external inputs of various timescales from the environment. How does the brain process this multitude of timescales? To answer this, we review recent studies. They show a hierarchy of intrinsic neural timescales (INT) with a shorter duration in unimodal (visual cortex, auditory cortex, etc.) and a longer duration in transmodal regions (default mode network, etc.). The unimodal-transmodal hierarchy is present in both shorter and longer timescales across acquisition modalities (EEG/MEG, fMRI), in both rest and task states, and across different species. Together, this evidence shows that the hierarchy of INT is central to temporal integration (joining/combining successive stimuli) and segregation (separating successive stimuli) of external inputs from the environment, including their prediction and prediction error.

The brain processes inputs of different timescales

Far from a passive experience, watching a movie requires complex skills. One must jointly consider the spoken language, visual effects, and background music, each of which contains a multitude of timescales. For example, language is comprised of words, sentences, and paragraphs that operate on a continuum of timescales, from shorter to longer [1]. We attribute meaning to language by temporally integrating words, sentences, and paragraphs, joining or combining those that come one after the other. Furthermore, we relate this to the background music we hear and the visual stimuli we see. How can the brain respond to this range of timescales and integrate them into one coherent whole? In this review, we explore how the brain (i) integrates – combines one stimulus after the other—and (ii) segregates – separates one stimulus after the other - different timescales from various environmental inputs.

Various studies observed that the brain carries **temporal receptive windows** (TRW; see Glossary). The concept of TRW was first introduced in 2008 [2] and, analogous to spatial receptive fields [3–6], refers to temporal windows through which the brain processes, i.e., integrates and segregates, information. These TRW process the temporal duration of ongoing inputs [7–14]. Specifically, **unimodal regions,** like the primary sensory cortices, process short duration stimuli such as words [1,11]. In contrast, higher-order or **transmodal regions**, such as the lateral and medial prefrontal cortex and the default-mode network (DMN), can process much longer segments such as whole paragraphs [1,8,10,11,13,15,16]. These findings, obtained in fMRI [1,2,11], EEG/ECoG [13,17], and single unit recordings [10], show that the brain's neural activity contains different timescales during task states which are related to different timescales in the external inputs.

In line with these observations, recent findings show that the brain's resting state (or spontaneous activity) also carries an elaborate intrinsic temporal hierarchy [10,12–14,18]. This hierarchy can be measured by the **autocorrelation window** (ACW), which computes the degree to which neural activity correlates with itself across its own various timepoints [3–5,9,10,19] (see Box 1 for different methods of calculating ACW). Unimodal regions show a shorter ACW than higher order cortical areas. In contrast, the higher-order transmodal regions exhibit longer timescales, thus a larger ACW [9,10,24,12–14,18,20–23]. This unimodal-transmodal hierarchy of the resting state's ACW is consistent with that of the TRW described above.

What is the role of these different **intrinsic neural timescales** (INT) in the brain's processing of external inputs? A central construct of interest in this review, INT serves as an umbrella term referring to the temporal durations, i.e., timescales, of the brain's neural activity. How are INT involved in the temporal integration and segregation of inputs (see [11] for the first study linking TRW and INT)? Do INT play a role in inferring future inputs, with an empirical prior and prediction error, as discussed in predictive coding [25]? In addressing these questions, we first review recent findings of INT on the system-level, i.e., network-level of the brain (Figure 1) in resting state and task states. Both rest and task states feature a unimodal-transmodal hierarchy of INT (see [19] for a discussion of the cellular basis of INT). Next, we discuss the role of temporal integration and segregation (see Glossary for a specific definition of these terms) of ongoing inputs, as well as how they are involved in producing an empirical prior. This is extended by highlighting how the implementation of INT is vital in brain-based robotics (Box 2), and outstanding questions (see Outstanding Questions).

Intrinsic neural timescales display unimodal-transmodal hierarchy

Hierarchy of timescales along unimodal and transmodal regions

INT have been investigated in both human and non-human species. Single-cell recordings in non-human primates revealed that, during the prestimulus interval [10], time windows (i.e., ACW) are longer in transmodal regions and shorter in unimodal regions (see also [3–5]). Unimodal-transmodal differences in ACW were confirmed in subsequent modelling studies that used either a non-human primate-based connectivity matrix [9,26–28] or a standard model of synchronization, i.e., Kuramoto model [29] (0.01 to 0.1Hz) (see also [30–34], below).

Are analogous unimodal-transmodal differences in INT present in humans? Indeed, a series of recent resting state fMRI studies support this. Using either small [11,35] or large-scale [4,12,18] fMRI datasets, longer ACW in transmodal regions of the central-executive networks (CEN), dorsal attention networks (DAN), and DMN have been observed. In contrast, unimodal regions exhibited shorter ACW. Interestingly, analogous temporal gradients in the ACW of subcortical regions such as the hippocampus have also been observed [18]. Interestingly, another study [18] observed analogous temporal gradients in the ACW of subcortical regions, such as the hippocampus. Together, these studies suggest that the hierarchy of INT along the unimodal-transmodal gradient is present in both non-human primates and humans during resting state activity in both cortical and subcortical regions.

In addition to these INT differences, resting state brain activity, especially in humans, has been investigated for its inter-regional functional connectivity (FC). FC can be calculated between regions in both unimodal and transmodal networks [36,37]. The measurement of INT, however, is based on intra-regional activity, as reflected in the ACW. This difference raises questions about the relationship between intra-regional ACW and inter-regional FC.

Two recent fMRI studies [12,18] addressed this relationship. They demonstrate a positive relationship between ACW and FC. Specifically, they found that longer intra-regional ACW is related to higher degrees of FC between that region and all other brain regions (see also [38–43]). Transmodal regions with longer ACW display stronger FC to other regions. In contrast, unimodal regions with their shorter ACW are less connected (FC) to other regions in both non-human primates [44] and humans [12,14,49,50,18,23,26,38,45–48] (see [51–57] for cellular- and population-based feedback mechanisms of inter-regional connectivity yielding intra-regional timescales; see also [3–5] and [19,28] for more details on the cellular basis of INT including excitation and inhibition).

Together, these findings show that the unimodal-transmodal hierarchy of short- and long-time windows holds across different timescales and modalities, i.e., single cell recordings, EEG/MEG, and fMRI, as well as across different species, i.e., non-human and human primates. Therefore, this supports the view that the unimodal-transmodal hierarchy of neural timescales is an intrinsic feature of the brain's temporal organisation that holds across different species. Moreover, INT are closely related to inter-regional FC, suggesting convergence of the brain's intrinsic temporal and spatial organisation [14,58].

Intrinsic neural timescales are modulated during task states

Does the unimodal-transmodal hierarchy of INT also shape neural activity during task states? A recent study using the Human Connectome Project data [14] examined the unimodal-transmodal hierarchy during resting state, as well as during three different task states (motor, **story-math** (see Glossary), and working memory). Using MEG, they demonstrated that the hierarchy of unimodal-transmodal (i.e., periphery-core) temporal differences in the ACW is also manifested in task states, thus exhibiting task-general or task-unspecific effects (see also [3]). Moreover, the resting state's hierarchy of ACW in unimodal-transmodal networks highly correlates (r - values of 0.8 to 0.9) with the unimodal-transmodal ACW distribution during all three task states. Finally, other studies show that the length of INT is directly related to the magnitude of task-related activity with regions exhibiting longer INT inducing higher task-related changes [12,59].

Are there also task-specific changes in the ACW? To measure this, a study [14] subtracted the ACW task cortical maps from the ACW resting state cortical maps to obtain task-related effects independent of the resting state. The subtraction yielded strong shortening of the ACW in transmodal regions, especially during the story-math task. No significant task-specific changes in ACW duration were observed in transmodal regions during the motor or working memory tasks. Interestingly, the reverse pattern was found in unimodal regions; here the ACW showed task-specific changes in motor and working memory but not in the story-math task.

How could one specific task like story-math shorten the duration of the ACW in transmodal regions, while maintaining the duration of the ACW in unimodal regions and vice versa in another task? Tentatively, we speculate that task-specific dissociations between unimodal and transmodal regions may be related to the temporal structure of the task itself, that is, its continuous (subsequent timepoints) versus discontinuous (discrete) nature [60]. For example, story-math is a more continuous paradigm (with 30s blocks) that requires longer timescales for integrating various inputs. In contrast, motor and working memory tasks are typical event-related discrete paradigms that recruit shorter timescales to achieve high temporal segregation [60].

These findings suggest that the different timescales of unimodal and transmodal regions may mediate the extent to which each region is able to accommodate the timescales and temporal structure of the task itself. More direct support comes from a recent EEG study [61]. They show that INT modulate the degree to which neural activity in alpha/beta, i.e., spectral power changes, relate to the input itself, in this case, a looming sound. The longer the ACW, the better stimulus-related alpha/beta power correlate with the physical intensity (dB) of a three second looming sound, and the faster the subject's reaction times in noting the sound [61]. Albeit tentatively, these and other data (see also [3–5,10,62] suggest a direct relationship between the length of INT with the temporal structure of the external input.

Together, these findings show the prevalence of the unimodal-transmodal hierarchy of INT during task states, thus shedding light on the possibility of studying the relationship between the duration of INT and the temporal structure of external task demands. Are INT thus key in mediating temporal integration and segregation of ongoing inputs during task states? This shall be the focus in the next section.

Intrinsic neural timescales shape cognition

Temporal receptive windows

Is there more direct evidence for a key role of INT in temporal integration [63–65] and segregation? Multiple empirical investigations [11,16,48,66–71] (see [7] for review) highlight the importance of INT in shaping cognition. These studies reveal that different brain regions mediate different timescales of the external stimulus, i.e., different regions may segregate or integrate the inputs according to different stimulus durations.

These studies showed that shortened temporal segments of external stimuli - single words of stories or short segments in movies - are processed preferentially in lower-order unimodal sensory regions. In contrast, longer intervals in the stimulus material - whole paragraphs in stories or longer segments in movies - are related to activity changes in higher order transmodal regions. In this way, continuous external input streams – a story or music – are segregated and integrated according to the temporal structure of different input durations.

Segregation and structuring of external input streams have been described by the concept of TRW. TRW refer to time windows of varying lengths in the brain's neural activity that are related to the length of sensory information, i.e., the duration of input features. For example, continuous sensory input streams from music or movies are segregated by the brain's INT into different temporal segments or time windows of shorter and longer duration [5,7,11,16,66].

Temporal segregation has also been complemented by temporal integration. For instance, single letters are combined into one word within a short time window in the shorter timescales of the unimodal cortex. However, the timescales of the unimodal primary auditory or visual regions are too short to combine several words into one sentence as that requires longer timescales. Combining words in sentences thus recruits regions such as the middle temporal gyrus (or even prefrontal cortex), which exhibit longer INT and are thus higher in the unimodal-transmodal hierarchy of INT [7] (Figure 2).

Together, these data strongly support the involvement of INT in temporal segregation and integration of input streams [29,59,72]. Specifically, shorter, and longer TRW in unimodal- and transmodal regions allow for temporal segregation and integration. As such, the brain attempts to match duration of INT with the duration of ongoing input streams (words, sentences, paragraphs etc.) [7,66–68,73,74].

Given that the unimodal-transmodal hierarchy of INT is preserved across different species, this allows for the exciting possibility of an evolutionary shaping and genesis [8,75,76]; the brain's connection to its respective environmental context, which manifests in its capacity for segregating and integrating inputs, may be a result of evolution. This is supported by the observation of analogous unimodal-transmodal hierarchies of INT on cellular [3–5,10], biochemical [77], and regional [14,18,23,78] levels of both human and non-human primates [75,76].

From temporal windows to cognition

INT have been associated with a variety of different forms of cognition in both non-human and human primates. Non-human primate data [10] shows that a longer ACW in the prefrontal cortex is associated with longer delays in a delay discounting task. Other non-human studies demonstrate that a longer ACW is associated with stronger spatial response coding in the delay period during a non-match-to-goal task [79], and modulates working memory performance during later periods, i.e., delay [44] (see also [3,80] and [19,81] for INT in perception and decision making).

In humans, recent fMRI and/or EEG studies demonstrate that the resting state's ACW is directly related to higher-order cognition, such as the level of consciousness [82,83], the sleep stage [84], the sense of self [85–88], and psychiatric disorders like schizophrenia and autism [22,35,89]. One study even measured INT during the drawing of different emotions - participants were instructed to draw the scenes of the following emotions (excitement, anger, depression, etc.) - which yielded different durations of ACW during subjects' drawing process [90].

TRW have been associated with process memory [7]. Process memory, a refined form of working memory, is based primarily on the temporal features that process memory contents (like longer or shorter duration) (see also [91] for a discussion of 'temporal memory' as distinguished from 'cognitive memory'). Other studies linked the INT to decision making [3,80] and the impact of reward on visual perception [10,19].

A recent review associates the longer TRW of transmodal regions with internally oriented cognition, while the shorter TRW of unimodal regions is more related to externally oriented cognition [8]. This association of the transmodal regions' longer INT with internally oriented cognition is supported by recent studies on the self and ACW. Applying fMRI [92] and EEG [85], it was observed that higher degrees of self-consciousness (as measured by the Self-Consciousness Scale) are related to longer INT in the resting state, especially in the cortical midline regions of the DMN. Longer INT indexing higher degrees of temporal integration thus appear to favor our internal self over the external non-self, i.e., environment, which, presumably requires stronger degrees of temporal segregation.

But is this association of self-consciousness related to higher degrees of temporal integration? This was addressed by a recent EEG study [87]. They first measured resting state activity and then conducted a psychological self-task. In this task, subjects were required to associate self- (geometric shapes previously assigned to the participants) and non-self-specific (geometric shapes previously assigned to other people) stimuli across different time delays (from 200 ms to 1400 ms). Their findings demonstrate that the self-specific effect of accuracy was preserved across all temporal delays, with inter-subject variation. That, in turn, was related to the length of the resting state ACW: the longer the ACW, the stronger the preservation of the self-specific effect across different time delays on the psychological level.

This suggests that temporal integration, especially of self-specific inputs across different timescales, is mediated by the length of INT. If correct, alterations in INT could lead to changes in cognition about one’s self. This is indeed supported by a recent EEG study in schizophrenia: subjects showed an abnormally long ACW which mediated their self-disturbances, including their relation to negative schizophrenic symptoms [89] (see also [90]).

The INT are also related to consciousness. Another EEG study [84] demonstrated that increasing loss of consciousness - N1 to N3 sleep during different degrees of sedation in anesthesia, and unresponsive wakefulness syndrome (UWS) - is related to an increase in the length of the ACW. In contrast, subjects who lost their motor function but preserved their consciousness (such as in locked-in syndrome and/or amyotrophic lateral sclerosis) did not show such lengthening of their ACW. Abnormally long INT have also been observed in fMRI of subjects in light and deep anesthesia and subjects with disorders of consciousness [82].

These studies suggest that even when not exposed to actual multiscale inputs from the external environment, the resting state still exhibits its own INTs, which index its capacity for processing potential inputs. Since they investigated only resting state activity, the ACW can only be indirectly related to specific input processing. However, converging these results with studies on task-related activity and INT [1,2,11,58,66,93] it is plausible to suggest that, when someone suffers a flattening of neural timescales to abnormally long durations, the ability to process inputs according to the normal temporal hierarchy, as well as a balanced relationship between segmentation and integration, is impaired or lost. This is, for example, the case in sleep where we can still be awakened at any time by sufficiently strong external inputs: the brain capacity or the predisposition to input processing is preserved [94,95]. In this regard, as Andrillon and colleagues have shown in their studies, neural activity related to the semantic content of stimuli is conserved in light NREM sleep, so that consciousness is not a necessary condition for several input processing activities (e.g., integration and segregation on the neural level). On the contrary, this remains impossible in total anesthesia and coma, where even the strongest external input will not awaken the individual, suggesting that the brain's capacity or predisposition for input processing is lost.

Together, these findings support the key role of INT in mediating temporal integration and segregation in higher-order cognition like process memory, self, and consciousness. Future studies are warranted to probe for specifically temporal integration versus segregation during different kinds of input constellations in the different forms of perception [96] and cognition (Figure 3).

Intrinsic neural timescales mediate temporal integration and segregation

From unimodal-transmodal hierarchy to temporal integration and segregation

What are the mechanisms through which the INT shape behavior and cognition? The observation of shorter TRW in unimodal and longer TRW in transmodal regions suggests a key role for temporal integration and segregation. Here, temporal integration refers to the summing of different inputs [58]: despite their occurrence at different timepoints, successive inputs are nevertheless lumped, or smoothed, together within one neural activity whose duration is based on the region's time window, i.e. its INT. Longer windows with longer INT, as in transmodal regions, will thus favor temporal integration. Hence, temporally distinct inputs lead to a temporally extended longer lasting neural activity change.

In contrast, temporal segregation refers to the degree to which different inputs at different points in time are separated in their respective neural activity. Here, temporally distinct inputs lead to temporally distinct, and thereby short, neural activity changes. This requires high temporal precision [58], which is favored by the shorter INT of the unimodal regions. Together, we suppose a close relationship between the length of INT and the duration of neural activity changes in response to inputs; this mediates the latter's temporal integration and segregation. One would expect that neural activity changes are generally short in unimodal regions whereas they may be longer in transmodal regions. This is indeed supported by computational models. Using a non-human primate-based large-scale computational model, the authors in [9] applied pulse input stimulation to the primary visual cortex. The computational results show that the activity in transmodal regions (here the anterior cingulate cortex) takes much longer to decay back to baseline resting state levels when compared to the rapid activity decay seen in unimodal regions (here the visual cortex). This converges with other computational modelling studies showing that a longer duration of ACW in rest is related to slower responses to external inputs such as TMS [29] or electrical stimulation [9,26] (when compared to a shorter duration of ACW).

Together, these computational results suggest that the differential timescales along the unimodal-transmodal hierarchy exert differential effects on the temporal duration and course of task-related neural responses to the same input. The shorter and longer INT of unimodal- and transmodal regions lead to shorter and longer task-related responses respectively.

In addition to the duration of the INT of a particular region, input duration can also be considered. Inputs of shorter and longer duration may exert a differential impact on unimodal- and transmodal regions as their task-related activity is driven by the different durations of their respective INT (Figure 4).

Together, these observations suggest that the different durations of the INT in unimodal- and transmodal regions are related to different durations in their task-related activity. These, in turn, favor different degrees of temporal integration and segregation of inputs whose duration, i.e., their input statistics, is also to be considered. Briefly, regions with longer INT favor temporal integration and longer-lasting inputs in particular. Regions with shorter INT tilt the balance towards temporal segregation with shorter-lasting inputs.

From temporal integration/segregation to prediction

Predictive coding (PC) is a theory in which the difference between an observation and its predicted value (the prediction error) is minimized through reciprocal interactions in a hierarchy of cortical areas [97]. This PC framework [25] suggests a ‘hierarchy of prediction’ [101,102] in the brain as higher order transmodal regions send a prediction to the next lower region. This prediction sent to the lower level is then compared to the observation at this level, and the prediction error (the difference) is produced. The prediction error from this lower level is then sent back to the higher level, where it adjusts the observation, which in turn changes the prediction. In this way, the hierarchy of top-down modulation [98–100] of lower-order unimodal regions from higher-order transmodal regions as postulated in PC [25] converges with the unimodal-transmodal hierarchy of INT.

As stated in a recent paper [101], findings suggest a ‘hierarchical feedforward-feedback cascade’. The inferior frontal cortex, which lies at the apex, yields top-down predictions to the superior temporal gyrus, which in turn sends prediction error signals back to the inferior frontal cortex (Figure 5) [103]. The cascade continues to the primary auditory cortex. In this way, the empirical prior in each level is the prediction from the previous level [25,104]. There is thus a hierarchy from transmodal to unimodal regions in the brain – we therefore speak of ‘transmodal-unimodal hierarchy of predictions’ (Figure 5).

How is the prediction hierarchy related to the temporal hierarchy of INT? In both temporal and prediction hierarchies, transmodal regions stand at the apex of the hierarchy while unimodal sensory regions are located at the base. This suggests a close relationship of the prediction hierarchy with temporal integration and segregation.

The longer timescales of transmodal regions, especially the DMN, are ideally suited for integrating different inputs over longer stretches or windows of time. That, as we tentatively suppose, may be key for yielding the empirical priors requisite for top-down modulation of lower-order unimodal regions. In contrast, unimodal regions exhibit shorter timescales which are ideal for segregating incoming inputs they receive from higher order transmodal regions, yielding a prediction error. Together, we assume that through different degrees of temporal integration and segregation, the unimodal-transmodal temporal hierarchy of INT is key for processing along the unimodal-transmodal hierarchy of predictions.

Albeit tentatively, we suppose that the timescales and their hierarchy of prediction may thus be strongly shaped by INT, the details of which remain to be determined. This would lend support to the notion of ‘deep temporal models’ or ‘temporal thickness’ [107] in the context of PC [31,107].

Concluding Remarks

Recent evidence from both humans and non-human primates demonstrates that the brain displays its own hierarchy of INT. Unimodal regions show shorter timescales while transmodal regions exhibit longer ones. This temporal hierarchy is present during rest and task states, where the INT have been described as ‘temporal receptive windows’. INT are also instrumental in mediating behavior and cognition-like processes (memory, self, and consciousness) including their different manifestations in unimodal- and transmodal regions. Together, these findings strongly point towards a key role of INT in temporal segmentation, with temporal integration and segregation of input streams. That, in turn, may provide a temporal underpinning of prediction, i.e., PC in its hierarchy.

The involvement of INT in behavior and cognition raises the question for the temporal structure underlying the latter. Do the INT structure and organize the contents of our cognition including mental features like self and consciousness [108]? The contents themselves may be strongly shaped by the balance of temporal integration and segregation mediated by the INT of the various regions and networks. Finally, the preservation of INT across different species raises the prospect that we, as humans, share how we process and thus temporally integrate and segregate environmental information to a certain degree. That suggests a deeper evolutionary origin of INT, including their unimodal-transmodal hierarchy. This, in turn, may allow for similar temporal integration and segregation of the shared environmental input streams across different species.

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Box 1: Different ways of measuring ACW and methodological considerations

The estimation of the duration and characteristics of the INT have been carried out with different methodologies. Most of these methods rely on the previous calculation of the autocorrelation function to later estimate its slope or its fall in different percentages, 50% and 0% [12,14,38]. However, there are other methods that, for example, are based on an analysis of the lag through a generalization of the Pearson correlation [18] or on the calculation of autoregressive models with exogenous inputs for the simultaneous estimation of multiple intrinsic timescales [3].

Yet another methodological issue is the frequency range within which the ACW is calculated. For example, the timescales considered in single cell recordings from non-human primates are much shorter than those of human fMRI, which operates in the range of 0.01 to 0.1Hz (100 to 10s). While the unimodal-transmodal hierarchy of INT has been well demonstrated in single cell recordings [3–5,10] and in the infraslow frequency domain of fMRI [12,18,22,23,35], the frequency range of EEG/MEG was yet to be determined. This gap was addressed in two recent MEG studies [14,26], which again show longer ACW in transmodal regions and shorter ACW in unimodal regions (Figure 2). Finally, it shall be noted that the ACW is usually computed across all frequencies (broadband), though it was recently computed in individual frequency bands in EEG [61]. In conclusion, despite the variety of the methods, modalities and frequency ranges used, all of these studies show similar hierarchy and topology in the neural patterns, which reinforce not only the robustness of these methods, but also the reliability of the results: INT and their hierarchy hold across different timescales.

Box 2: From INT to brain-based Robotics

Robots are equipped with sensors and actuators, giving them the capacity to navigate and continuously interact and align with the environment. However, these capacities would fall short under circumstances where the agent fails to carry the neural predisposition necessary to align with the input statistics from the environment, which ultimately carry multiple timescales – music is an example of multi-dimensional data. Is there a particular system design whereby its robotic implementation may ensure continuous matching/alignment with environmental stochastics?

To properly dance to the rhythm of the music, we propose that the implementation of INT in brain-based robotics can endow artificial agents with the ability to segregate and integrate multi-dimensional input statistics. The implementation of INT in robots may be achieved by constructing a deep multi-layered network that follows a unimodal-transmodal hierarchy (Figure IIA). Here faster and slower timescales would be associated with unimodal and transmodal layers respectively. Based on this topographic organization, the network may display a gradient a fast-slow timescales, with activity that is then directly linked to the agent's sensorimotor apparatus. In turn, this one-to-one correspondence between multi-layered network activity and behavior can be directly linked to the external inputs. For example, the embodiment of INT would provide the agent with the capacity to segregate and integrate external inputs according to their duration – directly assessing its ability to align to the rhythm of certain music features over others (Figure IIB). Finally, if the robot carries a limited number of timescales (e.g., single layer network with single frequency activity), the agent may fail to carry the neural predisposition necessary to align with the multitude of timescales of the music, thus dancing either too fast or too slow to the rhythm of the music.

Glossary

- **Autocorrelation window (ACW):** measures temporal integration in the time domain as the full-width-at-half-maximum (FWHM) of the autocorrelation function.
- **Input processing:** the concept of input can be understood more precisely by referring to sensory or exteroceptive inputs from the external environment (visual, auditory, or somatosensory inputs). A wider meaning would also include the input from the own body, the interoceptive input. Finally, resting state spontaneous brain activity can serve as internal input, e.g., auditory hallucination and dreams.
- **Intrinsic neural timescales (INT):** refers to temporal windows of neural activity during which neural activity is strongly correlated with itself. They are intrinsic to the brain because they are present in the resting state, independent of task-evoked activity. Moreover, the different brain regions (unimodal, transmodal) exhibit different durations

in their temporal windows; therefore, one can speak of multiple timescales in the brain's neural activity.

- **Neural predispositions of consciousness (NPC):** refer to necessary but insufficient neural conditions of consciousness; the neural correlates of consciousness (NCC) are sufficient for the actual manifestation of consciousness.
- **Predictive coding (PC):** an instance of active inference referring to the capacity to predict a forthcoming input, the empirical prior, which is then compared with the actual input, thereby yielding a prediction error.
- **Story-math task:** Human Connectome Project (HCP) task containing an auditory story presentation (5-9 sentences adapted from a colletion of Aesop's fables) with questions and math problems (simple addition/subtraction problems). The approximate length of the full story-math recording was 3.8 minutes.
- **Temporal prediction:** refers to the capacity to predict the next input; longer INT may yield an earlier prediction of the next input than shorter INT. The length of INT can influence the predictability of the next input with longer timescales potentially yielding an earlier prediction (Box 1).
- **Temporal receptive windows (TRW):** refer to the duration of meaningful external inputs like words (short), sentences (longer), and paragraphs (very long). The INT may provide temporal windows that receive and process inputs of different durations (see main text for details and references).
- **Temporal integration:** refers to summing of different inputs at different timepoints of neural activity based on specified regional timescales (sentences may be pooled together within one paragraph by one long time window of neural activity).
- **Temporal segregation:** refers to the parsing of different inputs at different timepoints of neural activity based on specified regional timescales (a sentence may be parsed into words and ultimately letters by short time windows of neural activity).
- **Transmodal regions:** cortical regions that process inputs from different sensory modalities (visual, auditory, etc.) including higher-order regions (prefrontal cortex).

- **Unimodal regions:** cortical regions that are lower-order sensory regions (primary/secondary visual cortex, auditory cortex). They are defined by processing exclusively inputs of one sensory modality (visual, auditory, etc.).

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Figure Legends:

Figure 1: Intrinsic neural timescales (INT). Top shows a schematic view of various timescales present in the brain (repertoire of timescales) alongside their unimodal or transmodal hierarchy (little red circles in brains). Increase in the length of the timescales is associated with their position in the spatial hierarchy of the brain. Bottom shows a schematic view of the role of intrinsic neural timescales in temporal segmentation including both temporal integration and segregation as well as prediction of inputs. The input contains different timescales (first box); for example, if the input is a paragraph in a book, the paragraph contains shorter timescales (syllables, words) and longer timescales (sentences). The input is segregated using these timescales (second box), and each timescale in the input is matched to a timescale in the brain through temporal integration (third box). Continuing with the example of the paragraph, the syllables and words are matched to the shorter timescales in your brain while the sentences are matched to the longer timescales in your brain. The combination of temporal integration and segregation yields the prediction error (fourth box). The prediction error, therefore, is the difference between the relevant timescale in your brain (shorter timescale) to the related timescale of the input (words).

Figure 2: INT across the unimodal-transmodal axis. Top left: the timescales (ACW) in an EEG topographical plot of the brain. Healthy controls data previously published in [109]. Top right: the hierarchy of timescales in an fMRI spatial map [14]. Bottom: the schematic illustration of INT across the unimodal-transmodal axis of the brain.

Figure 3: Temporal segmentation with temporal integration and segregation according to different repertoires of neural timescales in different states. This is an attempt to converge the results of various studies [1,2,11,58,66,83,84,93,94]. The ACW shows the different lengths of the INT repertoire and its topographic distribution. In awake and healthy subjects (A), the wide repertoire of timescales and balance between long and short INT correspond to sampling the input statistics in a fine-grained and temporally differentiated way; every detail of the chase scene is parsed across multiple levels of duration. Long segmentation: the integration of the two lines in the dialogue; mid-level segmentation: the distinction of the lines and the structure of the sentences; short

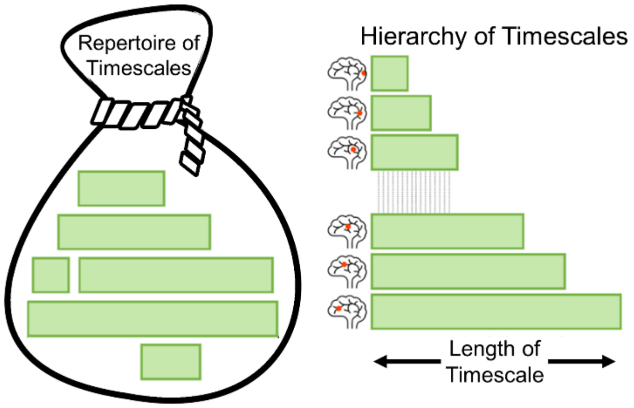
segmentation: the ability to separate and select every single word or syllable. Instead, in different sleep stages such as N1 (B), N2 (C), and impaired states of consciousness or under anaesthesia (D), the ratio between long and short INT becomes unbalanced, as the ACW shows a progressive reduction of the INT repertoire towards abnormally longer timescales. This corresponds to the loss of ability to segment the input series in detail, resulting in the coarse-grained integration of all stimuli into long time windows. From a phenomenological perspective, this consists of lumping together all words of the dialogue, as well as all frames of the scene, until the subject is no longer able to segment and process the stimuli in any temporal order and duration (as in deep anaesthesia and severe disorders of consciousness).

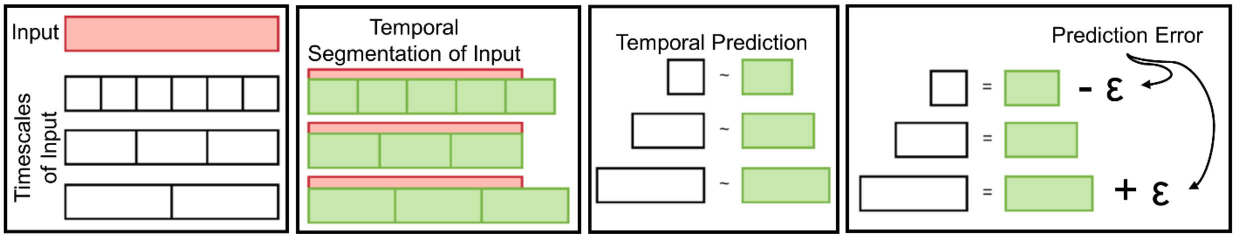
Figure 4: Input segregation-integration along the unimodal-transmodal hierarchy. A: Successive pulse inputs to primary visual cortex (V1) are differentially processed along the unimodal-transmodal hierarchy. Here, unimodal regions separate successive inputs while transmodal regions join or combine them (top). Schematically, area V1 treats the inputs as three distinct instantiations while anterior cingulate cortex (area 24c) treats them as a single instantiation (bottom). B: During a single pulse input of long duration, area V1 activity is fast-acting at input onset and short-lasting at input offset, whereas area 24c is slow-acting and long-lasting, respectively. C: Fast frequency activity in area V1 (purple inset) yields shorter ACW relative to the slow frequency activity in area 24c (red inset), which yields longer ACW.

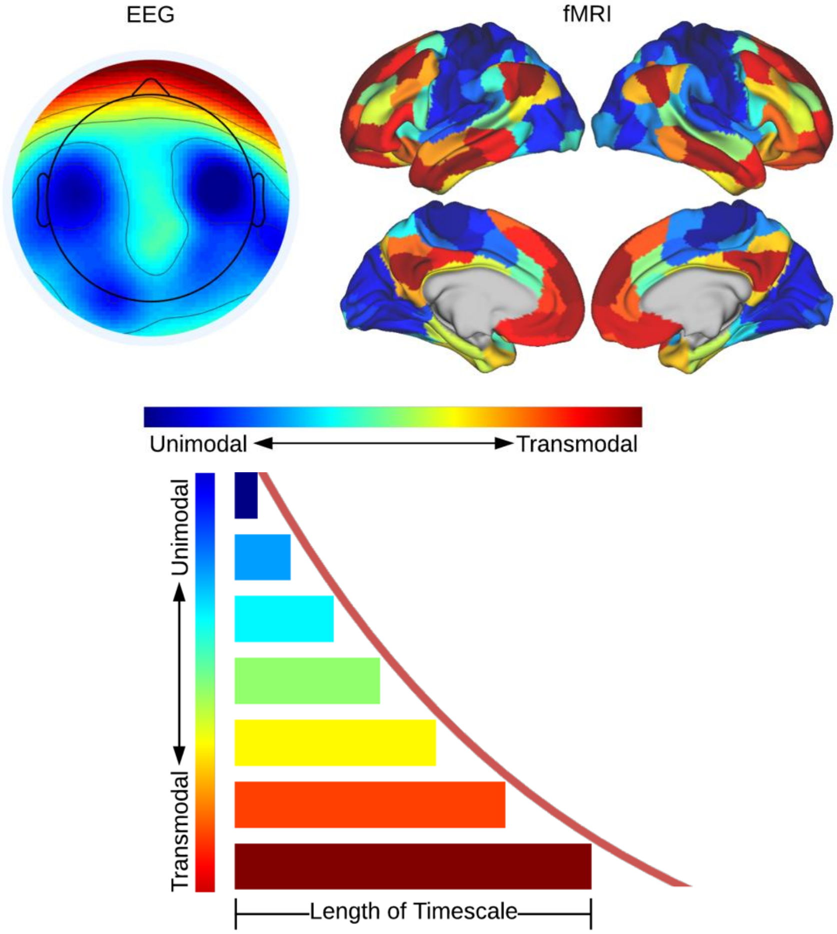
Figure 5: Hierarchy of cortical areas (feedforward-feedback cascade) and timescales related to Predictive Coding [101]. Primary cortical areas (e.g., early auditory cortex) receive external sensory input (music notes). The number and repertoire of timescales in this primary sensory area is large. At the top of the hierarchy (inferior frontal cortex), higher order areas have a smaller number and repertoire of timescales. In this 'feedforward-feedback cascade' [101], higher order areas provide 'top-down predictions' to lower order areas. At the same time, these higher order areas receive prediction error signals from lower order areas [103].

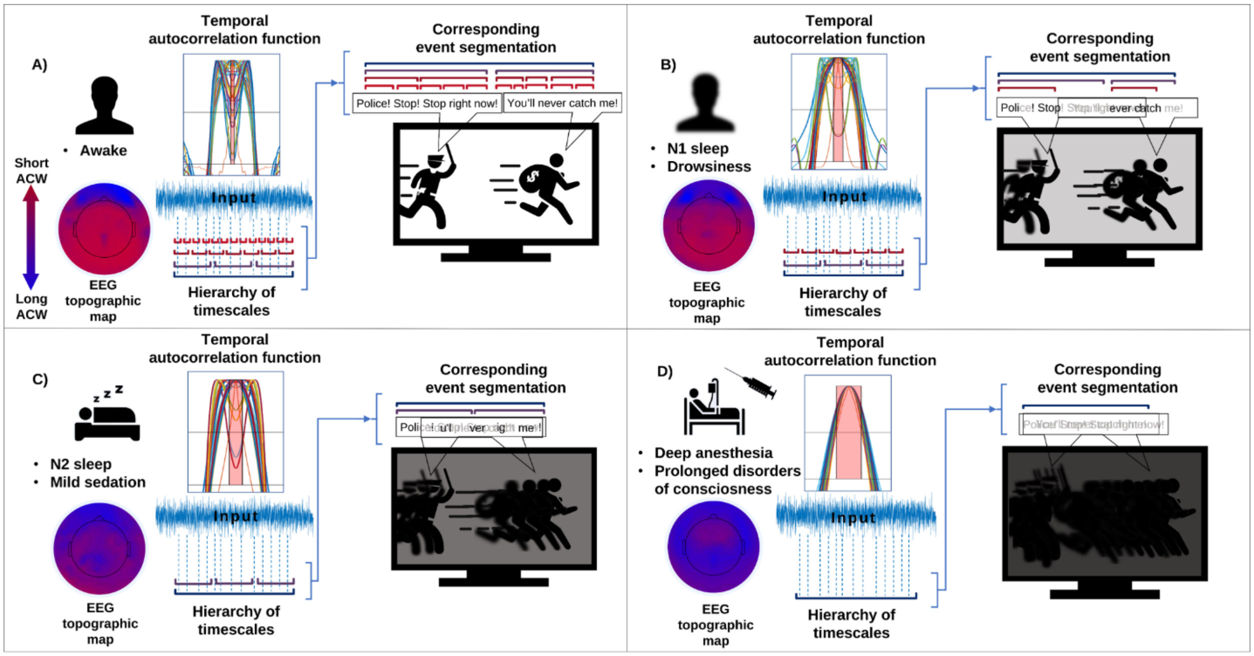
Figure I: Implementation of INT in brain-based robotics using deep multi-layered networks. A: Robots can carry multimodal sensory and motor capacities, making them suitable candidates for embodying a hierarchical organization of INT that follows the unimodal-transmodal hierarchy. B: Input segregation-integration can be directly tested in these agents, particularly in dynamic settings such as in music, which carries multiple timescales. As such, robots that operate only over fast timescales may carry the capacity for segregating music features, but not for integrating them. Consequently, the agent may dance too fast relative to the rhythm of the music (left). In contrast, robots that only exhibit slow frequencies would dance too slowly, missing out on the input processing of faster rhythms (middle). Finally, constructing a robot that carries both slow and fast frequencies would allow for both segregation and integration of input statistics, thus enabling the agent to dance to the rhythm of the music (right).

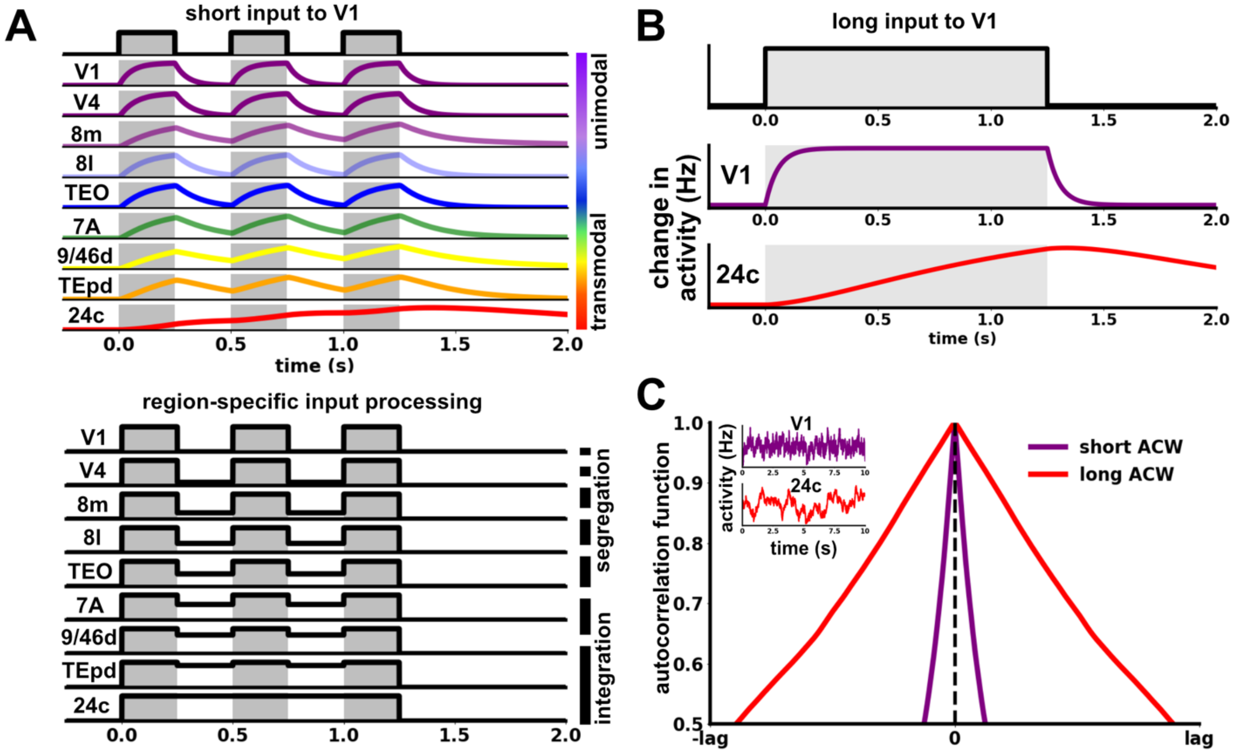
Figures:

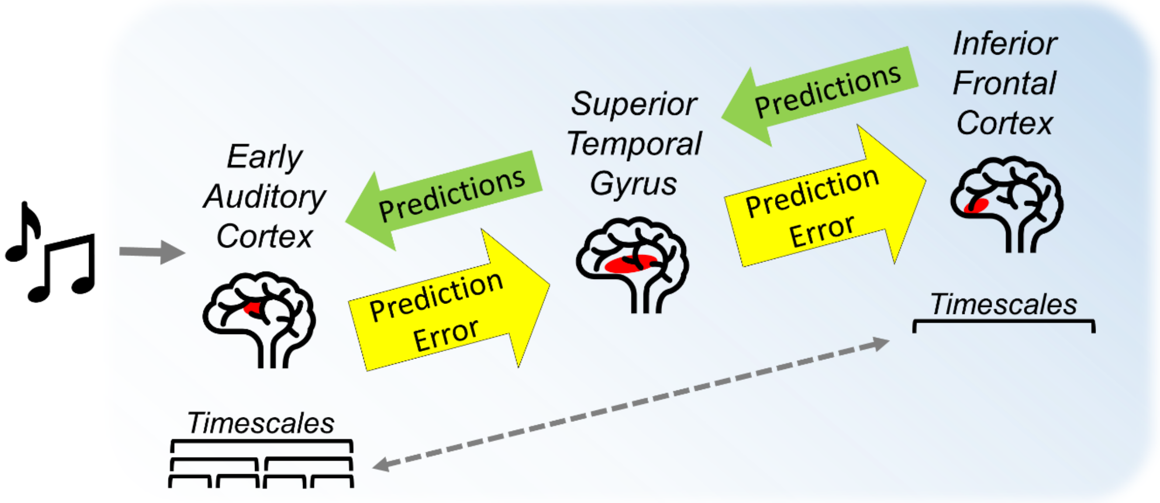

Repertoire of Timescales
Hierarchy of Timescales
Length of Timescale


Input
Timescales of Input
Temporal Segmentation of Input
Temporal Prediction
~
Prediction Error
=
- ε
+ ε


EEG
fMRI
Unimodal
Transmodal
Unimodal
Transmodal
Length of Timescale


A)
Temporal autocorrelation function
Corresponding event segmentation
Police! Stop! Stop right now!
You'll never catch me!
Awake
Short ACW
Long ACW
Input
EEG topographic map
Hierarchy of timescales
B)
N1 sleep
Drowsiness
Temporal autocorrelation function
Corresponding event segmentation
Input
EEG topographic map
Hierarchy of timescales
C)
N2 sleep
Mild sedation
Temporal autocorrelation function
Corresponding event segmentation
Input
EEG topographic map
Hierarchy of timescales
D)
Deep anesthesia
Prolonged disorders of consciosness
Temporal autocorrelation function
Corresponding event segmentation
Input
EEG topographic map
Hierarchy of timescales


A
short input to V1
V1
V4
8m
8l
TEO
7A
9/46d
TEpd
24c
unimodal
transmodal
0.0
0.5
1.0
1.5
2.0
time (s)
region-specific input processing
segregation
integration
B
long input to V1
change in activity (Hz)
V1
24c
time (s)
C
autocorrelation function
1.0
0.9
0.8
0.7
0.6
0.5
-lag
0
lag
short ACW
long ACW
activity (Hz)
time (s)
0
2.5
5
7.5
10



Ref: Dürschmid, S, et al. (2019) Direct evidence for prediction signals in frontal cortex independent of prediction error. Cerebral Cortex 29, 4530-4538.