



Review

Information flow dynamics in the brain

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Abstract

Timing and dynamics of information in the brain is a hot field in modern neuroscience. The analysis of the temporal evolution of brain information is crucially important for the understanding of higher cognitive mechanisms in normal and pathological states. From the perspective of information dynamics, in this review we discuss working memory capacity, language dynamics, goal-dependent behavior programming and other functions of brain activity. In contrast with the classical description of information theory, which is mostly algebraic, brain flow information dynamics deals with problems such as the stability/instability of information flows, their quality, the timing of sequential processing, the top-down cognitive control of perceptual information, and information creation. In this framework, different types of information flow instabilities correspond to different cognitive disorders. On the other hand, the robustness of cognitive activity is related to the control of the information flow stability. We discuss these problems using both experimental and theoretical approaches, and we argue that brain activity is better understood considering information flows in the phase space of the corresponding dynamical model. In particular, we show how theory helps to understand intriguing experimental results in this matter, and how recent knowledge inspires new theoretical formalisms that can be tested with modern experimental techniques.

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“Life, said Samuel Butler, is like giving a concert on the violin while learning to play the instrument. That, friends, is real wisdom.”

Saul Bellow, “My Paris,” 1983.

1. Introduction

1.1. Why dynamics?

When we think about information processing in the brain it is useful to paraphrase Butler and Bellow as follows: brain activity is like playing a violin in a concert while learning to play and creating the score as you are playing. To do this the brain has to sequentially use cognitive functions such as perception of auditory information produced by the violin, unsupervised learning of playing, working memory to remember the part of the concert already performed, decision making to choose the strategy for the next move, attention to keep the line of strategy, score creation for the following step and, finally, generation of a motor program for the action. In other words, brain information processing includes: information perception, transduction, coordination, storage, and information creation. All of these processes are dynamical and correspond to the continuous change of the underlying brain states, even in a constant environment.

As some multielectrode recordings and imaging experiments suggest, brain information dynamics can be considered as a sequence of controllable instabilities. Transient brain states that reflect the stabilization of one instability and, coincidentally, the emergence of another can be described as metastable states. Learning and generating ordered sequences of metastable states is a core component of information flows in the brain.

Let us illustrate the specificity of cognitive information flows on an example of a decision making (DM) task proposed by J.J. Anderson [1]. The cognitive approach to DM is different compared with the classical information theory approach to DM because it is cast as a problem in optimization of uncertainties and costs of different alternatives. From the cognitive perspective, DM is a dynamical process in which a temporally varying noisy information flow is integrated across multiple time scales with a decision resulting when the information flow relevant of one of the alternatives reaches a certain threshold. While the game theoretic approach will identify the optimum decision, the cognitive paradigm has a neurological basis but is often biased depending on the context in which the information is used. Thus, the cognitive approach is the most realistic. Because the cognitive approach is dynamical, it can address the biases and stability conditions in real-time DM where time dependencies may prematurely terminate the decision process externally. Throughout this paper we will emphasize the role of dynamics in different types of brain information processing.

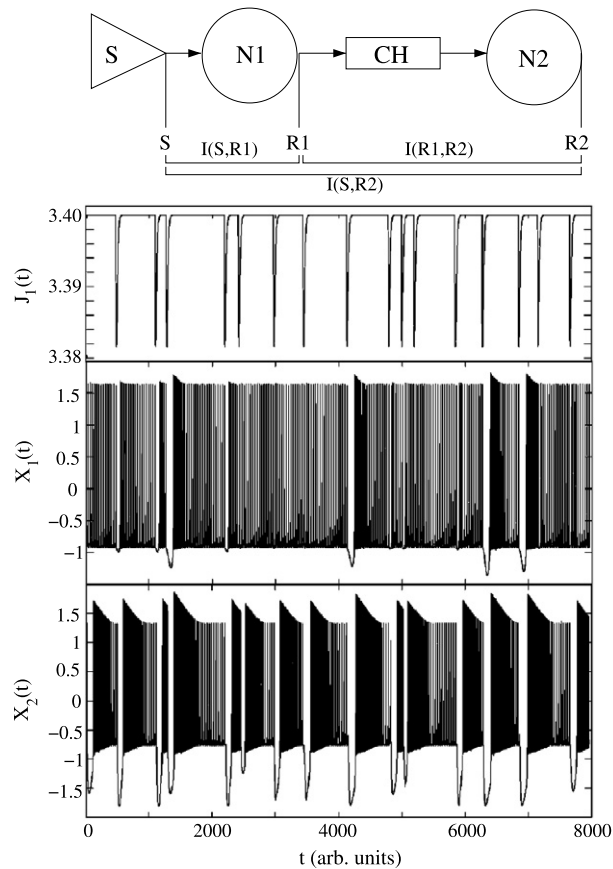


Fig. 1. Example of recovery of hidden information between two neurons. Top panel: the synaptic stimulus S is injected into the bursting neuron $N1$ that is unidirectionally coupled to a second bursting neuron $N2$ through an excitatory chemical synapse CH . Bottom panel: Time series of the synaptic input $J_1(t)$, the membrane potential of the first neuron $X_1(t)$ and the membrane potential of the second neuron $X_2(t)$ in a model described in [5].

1.2. Information processing by active dynamical networks

In a passive information processing system, sensory information is processed according to certain learning and association rules and then bound into a representation, which is stored, retrieved and matched with new incoming representations. In neural networks that can be considered as active dynamical systems, most of the information perception begins with the emergence of a goal that is implemented by the search for information. The processing channel itself can be a complex, even chaotic, dynamical system [2]. The only input accepted is that which is consistent with the goal and anticipated as a consequence of the searching actions [3,4]. Active neuronal systems demonstrate a lot of interesting information processing phenomena which some times appear to be in contradiction with the traditional view or with the intuition. Let us consider here some examples.

1.2.1. Recoverable hidden information

In [5] and [6], the authors studied a nonlinear transformation of information flow in a neural channel with model neurons having chaotic intrinsic dynamics (see Fig. 1). In [6] models of spiking–bursting neurons were implemented in simple analogue circuits, and synaptic connections were realized both in analogue circuits and through a dynamic clamp software. The information input to the first chaotic neuron (EN1) in the channel emerges in its output partially absent and partially ‘hidden’. Some part is absent because of the dynamical effects of the chaotic oscillation that effectively acts as a noisy channel. The ‘hidden’ part is unexpectedly recoverable by the second neuron (EN2). It has been shown that the synaptic parameters, most significantly the receptor binding time constants, can be tuned to enhance the information transmission by the combination of the action of the neuron and the synapse. The dynamics of

the synapse can be used to recover ‘hidden’ information using average mutual information as a measure of the quality of the information transport. Thus, the input signal may be hidden at one processing stage only to be recovered at a later stage, which is impossible in passive information channels. The observed results also indicated that information could be encoded in spike trains at vastly different temporal resolutions (see also [7]).

1.2.2. Multifunctionality

Usually neural networks are multifunctional. They are able, for example, not only to transduce sensory information, but also to generate new information depending on a specific context. Let us illustrate this phenomenon by describing the dual role of the gravimetric sensory organ of the mollusk *Clione limacina* [8,9].

During routine swimming, *Clione* maintains a vertical, head-up orientation. Any deviation from the vertical orientation produces a motor response directed to the restoration of the preferred head-up position. *Clione*’s orientation is determined by signals from the statocyst, the gravitational sensory organ. The statocyst is a sphere that contains a stone-like structure, the statolith, which moves inside the sphere under the effect of gravity. The statocyst internal wall is lined with statocyst receptor neurons (SRNs), which are mechanoreceptors responding to the pressure exerted by the statolith. The SRNs send signals to the cerebral ganglia where they affect the activity of cells controlling the motor neurons. Intracellular electrophysiological recordings from pairs of SRNs have shown that they are coupled with inhibitory nonsymmetrical connections. During routine swimming the statocyst network displays a winner-take-all dynamics: only those SRNs that receive excitation from the statolith are active to produce a command to return to the preferred head-up position.

Clione is a predator that has no visual system and during hunting behavior, its spatial orientation changes radically. In hunting behavior *Clione* constantly changes direction in an erratic search for prey. This behavior is evoked by a hunting neuron in the cerebral ganglia that excites the SRN network. The result is a winnerless competition (WLC) dynamics in this inhibitory network (see Fig. 2) that generates the program to organize the erratic search for prey [8,9]. A model study has shown that the quantity of the information generated by the statocyst in this case is characterized by the level of the dynamical instability and is equal to the Kolmogorov–Sinai entropy value (see [10]) or the summation of the positive Lyapunov exponents [11] (cf. Section 3.2). In spite of its irregularity, this type of activity contains activation phase locks that can guarantee coordinated motion [12,13].

1.3. Information generation – prediction, creativity, consciousness

Fortunately, there is no information conservation law in the brain. Because the brain is an active – non-equilibrium system it can create or generate information as a result of sequential instabilities. The quantity of such information can be characterized by the Kolmogorov–Sinai entropy and the quality of information depends on how it is adequate for the cognitive goal, i.e., what is the distance between the generated information and the optimal one in some sense. This is a very challenging and provocative problem.

In fact, information in cognitive science is determined differently depending on the problem. For example, the quantity of consciousness corresponds to the amount of integrated information generated by a complex of elements above and beyond the information generated by its parts [14]. The same approach can be used to understand creativity and imagination, which are the ability to combine together in many ways local brain instabilities in larger coherent patterns. The results have to be filtered, granting access to the working memory of only the most stable products of imagination and intuition (see also [15]).

One of the most interesting examples of relationship between local space–time instability, uncertainty and creativity is our everyday language. Suppose we are going to describe some subject – idea, situation or person. This can be done in many different ways and by using different words and linguistic structures. The chosen way depends on the personality, emotion, memory, etc. (see [15,16] and below).

1.4. Space and time – role of transients. Modeling of information flows

Neuroscientific research is often based on the assumption that neural mechanisms underlying perception and other brain functions can be inferred from steady-state measurements of neural activity or by models in which the behavior of the network is at steady state or periodic. In this view, computing with attractors is a familiar concept to the neuroscience community. In response to a stimulus, a neural network gradually changes its pattern of activation

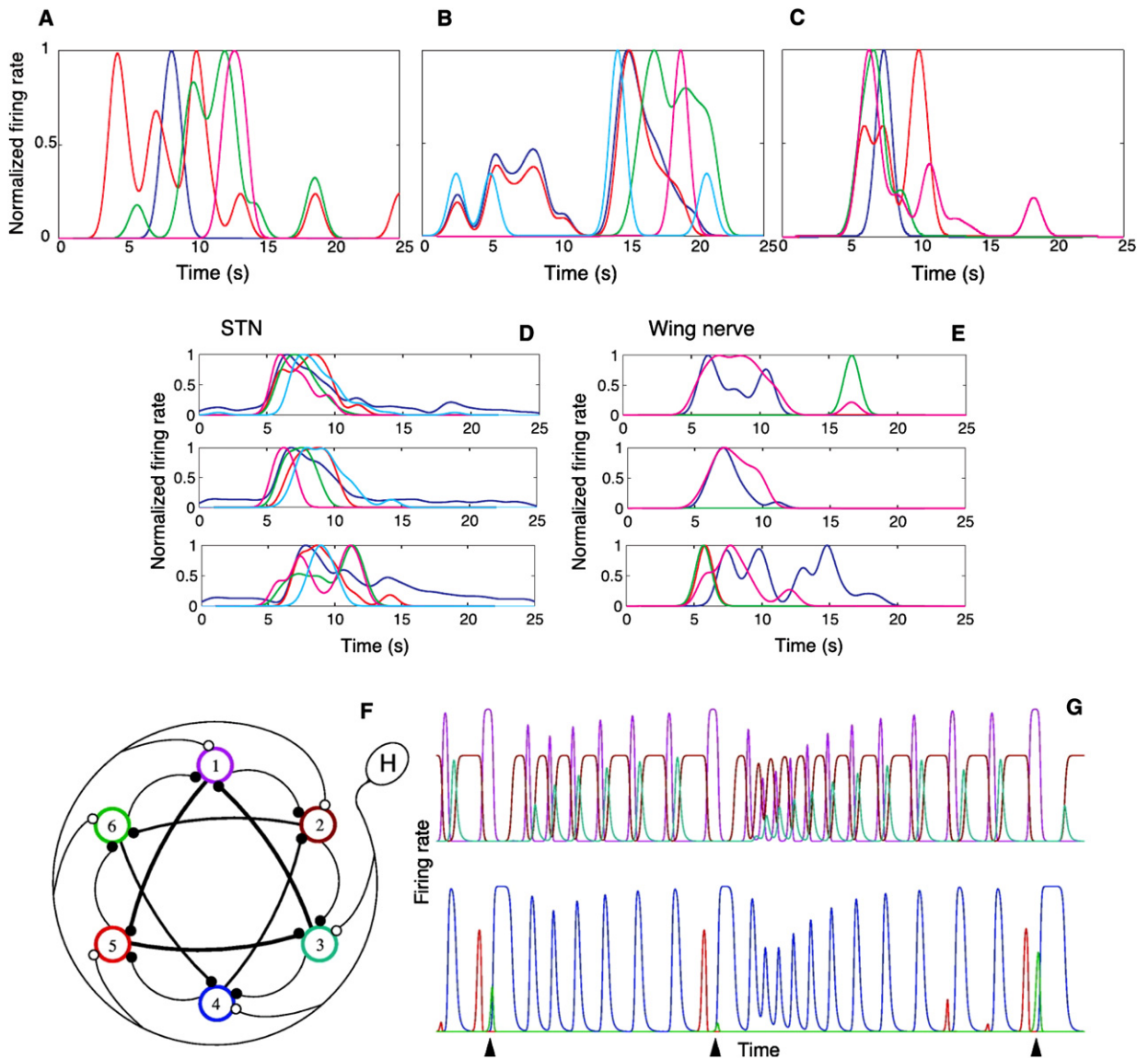


Fig. 2. WLC dynamics between sensory neurons in the mollusk *Clione*. Panels A–C: WLC firing pattern of SRNs during three hunting episodes. Each color represents an identified neuron, the spikes of which were detected and translated into spike density functions. Although the activity of several units can overlap, the temporal activation shown in this figure is sequential in the sense that the peaks of unit activity are distributed over the duration of the hunting episode. Similar spatiotemporal activity in the statocyst network corresponds to a similar pattern in the motor neurons. Panel D shows examples of normalized activity corresponding to 5 different SRNs during three episodes of hunting. Panel E shows the activity from wing motor neurons during the corresponding hunting episodes. Panel F displays a model of the statocyst network during hunting behavior. Panel G shows the chaotic WLC activity displayed in this model. Adapted from [8,9,11].

until it settles into one pattern, an attractor state. Thus, the input – a visual stimulus, a voice, an odor, or something more abstract – is associated with properties of the entire network in a particular attractor state. Such patterns of neural activity might be established, learned, and recalled during perception, memorization, and retrieval, respectively. However, recent experimental evidence and theoretical work shows that transient dynamics or transient states – ones in which no stable equilibrium is reached – can better represent information processing in the brain [17–22].

There are two fundamental contradictions regarding the use of transient dynamics for the description of brain activity. First of all, transient dynamics are inherently unstable. Any transient depends on initial conditions and cannot be reproduced from arbitrary initial conditions. Second, dynamical robustness can prevent sensitivity to informative

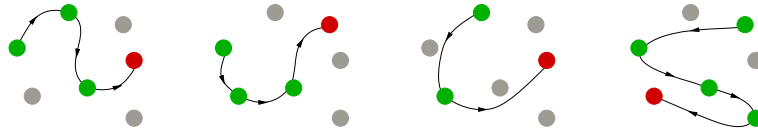


Fig. 3. Different information inputs (external or internal stimuli) are represented in the phase space by different sequences of global modes activity – different chains of metastable states. The specific topology of the signal-dependent information flow is a key feature that helps to solve a problem of information flow stability against stationary noise.

perturbations. If transients are reproducible in spite of the presence of noise, how can they also be sensitive to small informative signals? We will explain below how these contradictions can be resolved through the concept of metastability. This concept appeared in cognitive science at the end of the last century [23–29]. To describe robust transient dynamics, we need to introduce a mathematical image that is consistent with existing observations. Once we have this mathematical tool we can build models that can be used to reveal and understand the properties of this type of dynamics and generate testable predictions.

One plausible image of robust transients is a stable heteroclinic channel that consists of a sequence of metastable states [30,20,31] (see Fig. 3 and Fig. 6 below). Overall brain activity can then be described as $A(k, t) = \sum_{j=1}^N x_j(t)U_j(k)$ where the population (global mode) actions, achieved by synchronization of individual neurons or computing elements, is represented in $U_j(k)$ and the dynamics of the network is in the time course of $x_j(t)$, which are taken to satisfy dynamical equations of the form of kinetic equations, in particular, as the generalized Lotka–Volterra model that we will discuss below in Eq. (2). Thus, each metastable state indexed by i is represented in neuronal (physical) space by a distributed set of excited neurons participating in a given brain mode. Metastable states on the x_i axes, $x_i = \text{const} \neq 0$, are saddles [31].

2. Information loops in brain space

2.1. Cognitive information: bottom-up–top-down flows

For cognitive information, in contrast with classical communication systems, the information meaning (quality, semantic) is a key feature compared with the information quantity. Here to understand brain information processes we have to address context dependent information and goal dependent information. This means that the perception depends on ongoing cognitive activity and behavior. Bottom-up and top-down information flows coexist. Such flows produce closed functional loops. Feedbacks are necessary for the successful behavior in an evolving outside world and for the generation of new information based on cues from the intrinsic world.

Our brain is constantly trying to find meaning in associations, connections, data and patterns. We are trying to make it out of the information quantity that is being presented. We also try to connect new information to our past experiences and knowledge stored in our minds. When we find a pattern that is meaningful to us, we add it to our perceptual map. If it connects to the knowledge already stored in our minds, we learn. When we can make those connections, we get a sense of relief from the anxiety, confusion or stress that accompanies data, facts and figures. If we cannot connect it to past experiences, we feel a sense of confusion and are overwhelmed.

The feedback between sensory systems and the cortex is dynamical and to really learn something, the brain has to go internal in order to make meaning from the information quantity. Time is needed for this, of course. Sensory images, in particular visual images, contain only perceptual (physical) information, which can be discovered in an image and elicited for further processing. Semantic information is the result of the interaction of sensory information with a human brain that detects and interprets the image depending on the cognitive goal. This reminds the paradox of quantum measurement (see, for example, [32]). In quantum mechanics, measurement has counter-intuitive traits. In particular, properties of a quantum system found in a measurement may not exist before the measurement. Thus, a property found as the result of a measurement, i.e. the interaction, depends on the investigator.

Relying on a new definition of “information,” which can be derived from Kolmogorov’s complexity theory and Chaitin’s notion of algorithmic information [33,34], Diamant has proposed a framework for visual information processing, which explicitly accounts for perceptual and cognitive image processing peculiarities [35].

Information feedbacks are crucially important for consciousness. In a recent paper [36], the authors studied the differences between healthy and vegetative brains and conclude that damage to communication, i.e. to top-down

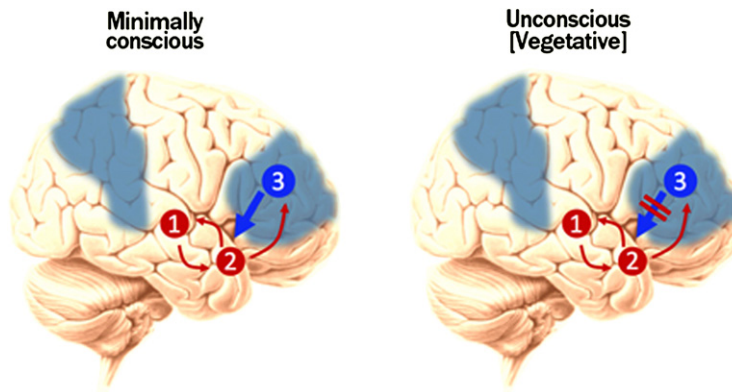


Fig. 4. The flow of information in the brain might be a crucial element of why patients in vegetative states cannot move or speak on their own accord. Signals can pass into the frontal cortex (area 3) – considered the brain’s decision-making center – but neurons there cannot send messages back out (adapted from [36]).

connections within the brain, is responsible for the transition to the non-consciousness – vegetative state. When healthy or minimally conscious brains registered unexpected noises, electrical signals passed from the brain’s auditory centers to the frontal cortex, which were transmitted back in a long-lasting loop. In vegetative patients, however, the loop was disrupted (see Fig. 4). According to Karl Friston’s theory, the frontal cortex learns to expect certain things – patterns of sound, for instance – and communicates those expectations to the rest of the brain. When those expectations are not met – e.g. the tone changes – the brain has to interpret surprising information. This result emphasizes the importance of top-down projections in recurrent information processing that involve high-order associative cortices for conscious perception [36].

2.2. Functional dependent informational flows

Fig. 5 illustrates the information flows involved in what Cisek has named as affordance competition hypothesis. This general hypothesis is related to a distinction between two types of information processing that animals face in real environments – deciding what to do and how to do it. Cisek [37] called these problems as action selection (decision making) and action specification (movement planning). For the particular case of visually guided movement, action specification (Fig. 5, dark blue lines) may involve the visual stream and a distributed and reciprocally interconnected network of areas in the posterior parietal and caudal frontal cortex [38]. These circuits perform transformations that convert information about objects in sensory coordinates into the parameters of actions. Along the way, each area can represent information about several potential actions simultaneously. Because multiple actions usually cannot be performed at the same time, there is competition between options, perhaps through mutual inhibition among cells with different tuning properties [39,40]. There are many other examples of competition between multiple brain systems (e.g. see [41]).

How large neuronal populations encode and process sensory information is a challenging problem in cognitive neuroscience [42]. In the paper [43], authors presented a novel application of computational methods to the integration of neural processes at the systems-level scale. The central result of their study is that sensory-motor interaction and body morphology can induce statistical regularities and produce information patterns in sensory inputs and within the neural control architecture. Using nonlinear time-series analysis techniques, they have investigated how the flow of information between sensors, neural units, and effectors is actively shaped by the interaction with the environment. This study represents an important step towards the development of an explicit quantitative framework that unifies neural and behavioral information processes.

Serial sensory processing information flows are working in parallel. For example, while information proceeds from primary (SI) to secondary (SII) somatosensory cortex in a serial fashion, both areas are known to receive direct thalamocortical sensory input. Authors in [44] examined the potential roles of such parallel information flows. They showed that the human brain can utilize parallel information inputs to facilitate long-distance cortico-cortical connections,

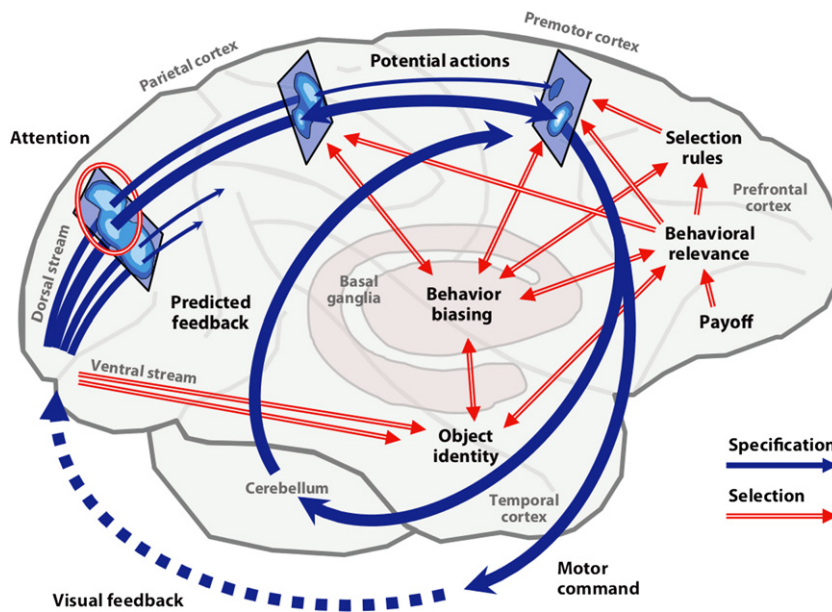


Fig. 5. The primate brain is shown, emphasizing the cerebral cortex, cerebellum, and basal ganglia. Dark blue arrows represent processes of action specification, which begin in the visual cortex and proceed rightward across the parietal lobe, and which transform visual information into representations of potential actions. Polygons represent three neural populations along this route. Each population is depicted as a map where the lightest regions correspond to peaks of tuned activity, which compete for further processing. This competition is biased by input from the basal ganglia and prefrontal cortical regions that collect information for action selection (red double-line arrows). Modified from [40]. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

resulting in accelerated processing and speeded reaction times. This mechanism could also allow very early top-down modulation of the bottom-up stream of sensory information.

What are the mechanisms of task dependent effective brain connections? There are several interesting hypotheses discussed in last few years. The main problem is that fast connection changes are incompatible with the slow variation of anatomical connections. Thus, such changes can be realized just as transitions in the cooperative dynamics of neural networks. For example, in [45] authors have analyzed small networks – motifs of interacting cortical areas, modeled first as mean-field rate units and also as large populations of spiking neurons. Local couplings in these motifs are mainly inhibitory while longer-range couplings are purely excitatory. All the interactions are delayed and structural networks are fully symmetric. Such motifs generate oscillatory patterns, which spontaneously break the symmetry under permutation of the areas and can give rise to multiple alternative effective networks with reduced symmetry, in which the inter-areal flow of information is anisotropic.

A similar idea is discussed in [46]. Rhythmic oscillations generated by brain networks can be a key component of the dynamical mechanism of profuse interregional connectivity in mammalian brain. Authors in [47] showed that switching one of several convergent pathways from an asynchronous to an oscillatory state allows accurate selective transmission of population-coded information. They suggested a mechanism for task dependent signal routing in neural circuits, which exploits sparsely synchronized network oscillations and temporal filtering by feed-forward inhibition.

3. Evolution of information in time: flows in phase space

3.1. Mathematical image

A stable heteroclinic channel is the mathematical image of robust transient dynamics and is defined as a sequence of successive metastable (saddle) states. These saddles can be pictured as successive and temporary winners in a never-ending competitive game (see right panel in Fig. 6).

The mathematical image that we have just introduced to discuss a paradigm of information flows in phase space does not depend on the geometrical structure of the neural ensemble in physical space. This paradigm can explain and

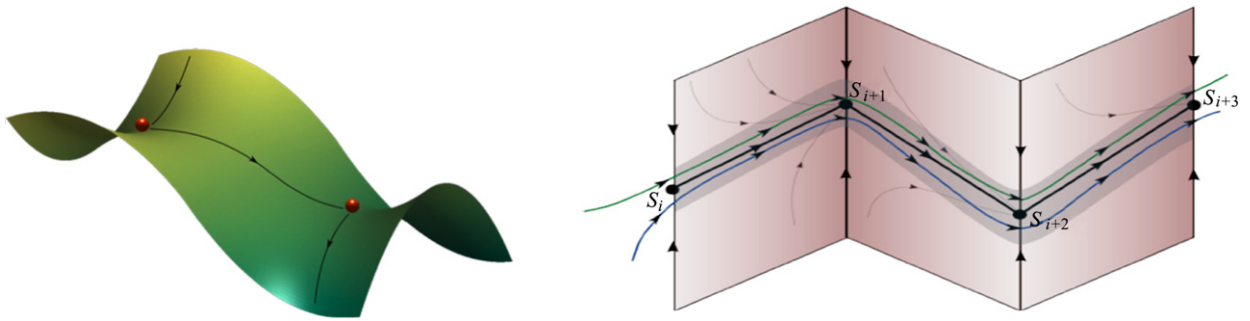


Fig. 6. Representation of a simple heteroclinic chain (left) and a robust sequence of metastable states (right). In the phase space of a dynamical model a temporal winner (metastable state) is represented by a saddle fixed point. Based on this landscape metaphor it is easy to see that two saddles can be connected by an unstable one-dimensional saddle separatrix (see the left panel). This is the simplest heteroclinic sequence. In many-dimensional phase space (multiple interacting modes) heteroclinic sequences with many connected saddles could exist and form, in a wide area of control parameter space, a stable heteroclinic channel – a stable heteroclinic flow (see right panel).

predict many dynamical phenomena in neural networks with excitatory and inhibitory synaptic connections including information transmission and generation. The paradigm is called winnerless competition (WLC).

The study of competitive dynamics has a long tradition. Survival of the fittest is a cliché that is often associated with the term competition. However, competition is not merely a means of determining the winner, as in a winner-take-all network with attractor dynamics. It is also a multifunctional instrument that nature uses at all levels of the neuronal hierarchy. Competition is also a mechanism that maintains the highest level of variability and stability of neural dynamics, even under transient behaviors. Nonlinear dynamical theory has furnished the concept of stable transients that are robust against noise, yet sensitive to external signals [48,31,49].

Stable transients, in fact, are a trajectory that is formed in the vicinity of a sequence of metastable states that are connected by separatrices as we illustrate in Fig. 6. Under proper conditions, all trajectories in the neighborhood of metastable states that form the chain remain in their vicinity, ensuring robustness and reproducibility over a wide range of control parameters. This vicinity is called Stable Heteroclinic Channel (SHC). SHC is possibly the only dynamical object that satisfies the dynamical principles of robustness and sensitivity in competitive world. During the last twenty years there have been several efforts to explain sequence generation with attractor networks based on synaptic delay and recurrent synaptic integration [50,51]. Some of such models provide interesting explanations but usually in very specific contexts.

To understand the conditions of the stability of heteroclinic channels, we have to take into account that an elementary phase volume in the neighborhood of a saddle is compressed along the stable separatrices and it is stretched along an unstable separatrix. Let us order the eigenvalues of the Jacobian at the i -th saddle point as:

$$\lambda_1^{(i)} > 0 > \operatorname{Re} \lambda_2^{(i)} \geq \operatorname{Re} \lambda_3^{(i)} \geq \dots \geq \operatorname{Re} \lambda_d^{(i)} \quad (1)$$

The number $\nu_i = -\operatorname{Re} \lambda_2^{(i)} / \lambda_1^{(i)}$ is called the saddle value. If $\nu_i > 1$ (the compressing is larger than the stretching), the saddle is named as a dissipative saddle. Intuitively it is clear that the trajectories do not leave the heteroclinic channel if all saddles in the heteroclinic chain are dissipative. A rigorous analysis of the structural stability of the heteroclinic channel supports this intuition [20].

The temporal characteristics of transients are related to the exit problem for small random perturbations of dynamical systems with saddle sets. A local stability analysis in the vicinity of a saddle fixed point allows to estimate the characteristic time that the system spends in the vicinity of the saddle as $\tau(p) = 1/\lambda_1^{(i)} \ln(1/|\eta|)$, where $\tau(p)$ is the mean passage time, $|\eta|$ is the level of noise, and $\lambda_1^{(i)}$ is the maximum eigenvalue corresponding to the unstable separatrices of the saddle.

To fully understand such structurally stable transient dynamics, we need to further describe the mathematical image of stable heteroclinic channels. Such dynamical objects are rare in low-dimensional systems, but common in complex ones. A simple model to describe these objects is a generalized Lotka–Volterra equation, which expresses and predicts the fate of an ongoing competition between $N \times M$ interactive neuronal modes:

$$\tau_i \frac{dx_i^m}{dt} = x_i^m \left(\sigma_i^m - \sum_{j=1}^N \rho_{ij}^m x_j^m - \sum_{k=1}^M \sum_{j=1}^N \xi_{ij}^{mk} x_j^k \right), \quad i, j = 1, \dots, N; \quad m, k = 1, \dots, M \quad (2)$$

where $x_i^m \geq 0$ represents the instantaneous amplitude of the (i^m)-mode, τ_i is a time constant, $\sigma_i^m \geq 0$ is the growth rate for the mode depending on an external stimulus, $\rho_{ij}^m \geq 0$ and $\xi_{ij}^{mk} \geq 0$ represent the asymmetric interaction strengths between the modes. Here m, k indicate different brain activity modalities, and i, j indicate different modes within the same modality. The parameters ρ_{ij}^m and ξ_{ij}^{mk} can depend on the stimuli. In the case of a single family modality, i.e., $M = 1$ we have the traditional Lotka–Volterra model. One of the remarkable features of this model is the existence in the phase space (for a wide range of control parameters) of a stable heteroclinic channel that corresponds to robust sequential switching from one metastable state to other [48,52,20,53].

Asymmetric inhibitory connection topologies help to solve the apparent paradox that sensitivity and reliability can coexist in a network [54,55,20]. To be reliable, a system must be both sensitive to the inputs and insensitive to perturbations and initial conditions. To solve this paradox, one must realize that the neuronal modes participating in a stable heteroclinic channel are formed by the stimulus, by virtue of their direct and/or indirect input from the neuronal modes activated by that stimulus. The joint action of the external input and a stimulus-dependent connectivity matrix defines the stimulus-specific heteroclinic channel. In addition, asymmetric inhibition coordinates the sequential activity of the modes and the strong compression of the elementary phase volume along the sequence keeps a heteroclinic channel stable.

3.2. Information flow capacity

When we try to understand brain activity from the perspective of information processing, we face two essential questions: (i) in which space do we have to consider such processing? and (ii) how is it related to the traditional probabilistic description of information? The brain's hierarchical organization [56], i.e., from the perception levels to the complex sub-core and cortex structures, supports the idea of an also hierarchical organization of its information flows. In fact, the popular view about the existence of one directional flows of sensory information (which are transferred through centers of preliminary processing to the cortex decision-making centers and behavior generation) does look very attractive. However, the reality is more challenging. As we have already discussed, the brain is characterized by a huge amount of informational feedbacks. This is a mechanism to control sensory input: by concentrating attention the brain chooses what sensory information is critical for executing cognitive functions to survive in a changing environment. However, the idea of a hierarchical organization of brain informational flows is very practical and promising [57], especially when we are talking about their temporal features.

Regarding the second question, the functional role of information (content and meaning) in cognitive processes cannot be directly measured with a traditional statistical approach. Although Shannon information [58] has made many valuable contributions and has many very important uses in neuroscience, it is somehow restricted to assess several functional properties of information, in particular the stability of the processes of information transmission and creation. Because the generation of, for example, a motor program or a speech need a sequence of signals, the information flow has to be organized in a specific temporal order that must be kept. In fact, such idea can be traced back to Wiener who recognized the importance of temporal ordering in the inference of causal relations [59]. Granger formalized Wiener's idea in terms of autoregressive models of time series [60]. However, we cannot directly use this idea because we first need to find an instrument for the quantitative analysis of informational flow dynamics.

Now let us provide a definition: we call a cognitive (mental) information flow a specific sequence of items. Note that it is not a number of items or events but a particular relationship between specific items ordered in time. In contrast to the traditional view, in order to understand the evolution of information in time we suggest to consider the informational flows in the phase space of a corresponding dynamical model, as an alternative to the physical space of the brain. In other words, an informational flow is a flow along a chain of metastable states. The end of the chain is a state corresponding to a final or intermittent decision or action. One of the critically important features of such informational sequence is its stability for recalling, which guarantees the usefulness of the sequential information (behavioral or cognitive). The information flow that we have just defined naturally satisfies the causal–answer relationship and is the basis for solving several problems that are related to overcoming uncertainty and to generating a decision – the new information. For cognitive processing a flow in a phase space – a spatiotemporal representation of information – is a natural way that provides continuity of the processing.

The quantitative description of information flows in phase space can be done by computing the sequence of mutual information along the heteroclinic channel between neighbor saddles. Another quantitative characteristic of an information flow along heteroclinic channels is the Information Flow Capacity (C_{IF}) – which changes along heteroclinic channel as:

$$C_{IF}(L) = \sum_i^L (\Delta C_{IF}(l)) \quad (3)$$

where

$$\Delta C_{IF}(l) = J_l + \sum_{j=1}^{J_l} \frac{\text{Re } \lambda_j^l}{|\lambda_{J_l+1}^l|} \quad (4)$$

Here l is the index of the metastable state (saddle) along a channel, L is the number of saddles that system passes until time t_L , λ_j^l are the eigenvalues of the Jacobian of the l saddle, and the integer J satisfies the following conditions ($\text{Re } \lambda_1 > \dots \geq \text{Re } \lambda_m > 0 > \text{Re } \lambda_{m+1} \geq \dots \geq \text{Re } \lambda_n$):

$$\sum_{j=1}^J \text{Re } \lambda_j > 0, \quad \sum_{j=1}^{J+1} \text{Re } \lambda_j < 0 \quad (5)$$

In other words, it is the number of eigenvalues at which the cumulative sum over real parts becomes negative. If the unstable separatrices of all saddles along the heteroclinic channel are one-dimensional, such that $J_l = 1$, we have:

$$C_{IF}(L) = \sum_l^L \left(1 + \frac{1}{\nu_l} \right) \quad (6)$$

In this case the ratio between positive and negative eigenvalues is equal to the saddle value ν_l in degree -1 (for the channel stability, the product of all saddle values has to be larger than one).

Put simply, the information flow capacity reports the average capacity to generate information through the constrained exponential divergence of trajectories as the system traverses its stable heteroclinic channel. This is reflected by the fact that it accumulates the number and relative sizes of the positive eigenvalues that report the dispersion of trajectories due to unstable flow.

3.3. Information binding. Fast recognition

Multisensory integration has often been characterized as an automatic process. Recent findings indicate that multisensory integration can occur across various stages of the stimulus processing that are linked to, and can be modulated by, attention. Stimulus-driven, bottom-up mechanisms induced by crossmodal interactions can automatically capture attention towards multisensory events, particularly when competition to focus elsewhere is relatively low. Conversely, top-down attention can facilitate the integration of multisensory inputs and lead to a spread of attention across sensory modalities. These findings point to a more intimate and multifaceted interplay between attention and multisensory integration than was previously thought [61].

Let us illustrate the usefulness of the C_{IF} for the quantitative description of information flows in brain. We will do it on an example of a heteroclinic binding problem. Multielectrode recordings from different areas of sensory systems in different animals suggest that sensory information on the first level of processing is encoded as spatiotemporal patterns by neural networks that implement a WLC interaction of different dynamical modes (variables) [18,62]. In the phase space, such dynamics is represented by a heteroclinic channel. Motivated by the multisensory dynamics observed in neural systems, authors in [63] have built a model that describes a network of heteroclinic channels binding the information representing different modalities (binding dynamics). This model is described by Eqs. (2) with $M > 1$ (see also Fig. 7).

Our interest aims to describe the neural dynamics associated with the binding problem in terms of a sequence of metastable states in the phase space. We have to remind that each metastable state indexed by i is represented in neuronal space by a distributed set of excited neurons participating in a given brain mode. We denote the i -th

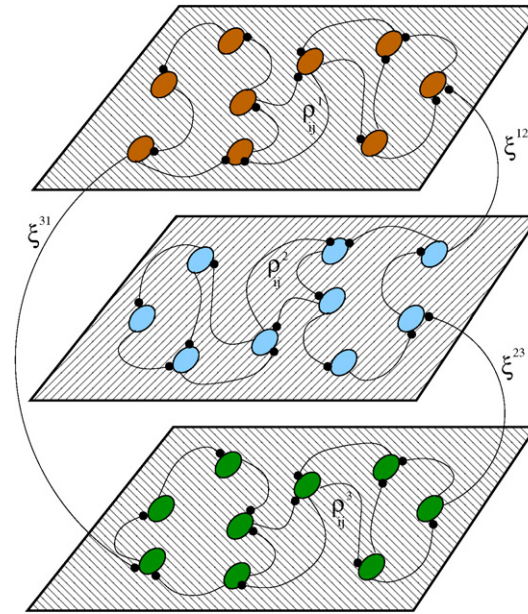


Fig. 7. Schematic representation of the interactions among WLC network of modes corresponding to three modalities. The dynamics of such network is described by the model (2).

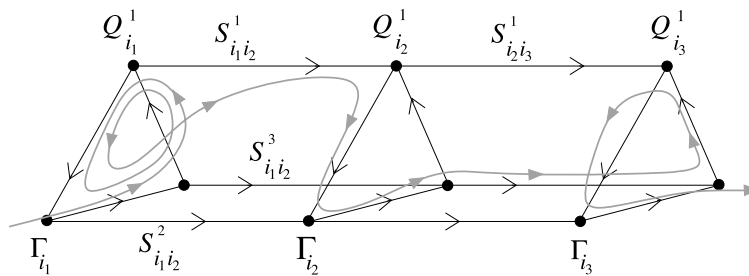


Fig. 8. Illustration of a multimodality heteroclinic sequence and a trajectory corresponding to the binding activity. The saddles are represented by the letter Q , the unstable separatrices by the letter S , and the stable heteroclinic contours by the letter Γ (for details see [63]).

mode as $x_i(t)U_i(k)$, where $U_i(k)$ is the normalized ratio of activity of the k -th member of the i -th set averaged in time and $x_i(t) \geq 0$ represents the level of the activity of the i -th mode. Such a set is the result of the temporal self-organization in a complex neuronal system. As we discussed in Section 1.4, metastable states on the x_i -axes, $x_i = \text{const} \neq 0$, are saddles. We suppose that the interaction between different modalities is weak. By keeping just the simplest nonlinearities we can suggest a phenomenological model of heteroclinic binding in the form of kinetic equations, in particular, as the generalized Lotka–Volterra model (2).

The main results of theoretical and computational analyses in [63] on this model can be summarized as: (i) for a wide range of control parameters, i.e., levels of excitation and inhibition, in the phase space of model (1), there exists an object that the authors named a network of heteroclinic channels (see Fig. 6), and the trajectories in the vicinity/inside of this dynamical object represent an integrated (binded) information flow of different modalities (see Fig. 8); (ii) the time series and spectrum of these multimodality-trajectories demonstrate new features – mutual modulation (see Fig. 9) and regularization of the different modalities and, correspondingly, the appearance of new components in the power spectrum of the activity. These properties displayed by the model can be key features for the next step of multimodality information processing, such as object recognition, speech generation, etc.

In fact, the heteroclinic binding is a way for transient self-organization of perceptual spatiotemporal modes. The information about the recognizable image coded by such modes can be transferred to the cognitive and behavioral modes for the next processing stage. We suggest that this phenomenon could be analyzed experimentally on fMRI data (see for rev. [64]).

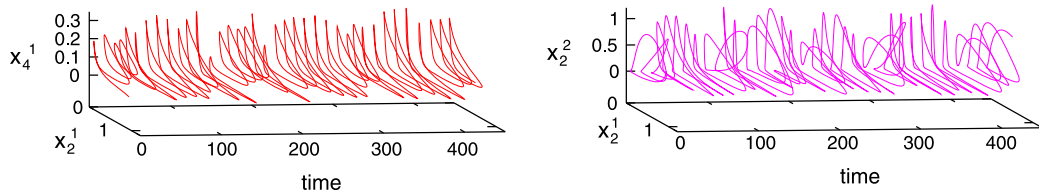


Fig. 9. Mutual modulation due to the heteroclinic binding of three coupled modalities built with three 6-mode networks. The modulation is illustrated by the joint time evolution of x_{21}^1 and x_{41}^1 (amplitudes of mode 2 and 4 in modality 1, left panel), and the joint time evolution of x_{21}^2 and x_{22}^2 (corresponding mode amplitudes in two modalities, right panel). Adapted from [63].

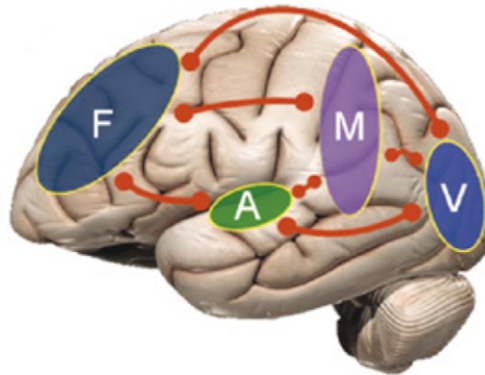


Fig. 10. The neural synchrony hypothesis: it is likely for sensory information processing in complex environments that multisensory interactions will combine into a unified pattern involving frontal cortex, temporo-parietal regions as well as unimodal cortices: A = auditory cortex; V = visual cortex; M = higher-order multisensory regions; F = prefrontal cortex (adapted from [68]).

As illustrated in Fig. 8 each saddle along a binded heteroclinic network has two unstable separatrices. This means all $J_l = 2$. Thus, the $C_{IF}(L)$ estimation described above tells us that the flow capacity for a binding channel is at least two times larger than the flow capacity of three independent channels. We can interpret this result in the following manner. Information flow capacity characterizes the complexity level of the trajectories within a network of heteroclinic channels. One can say that such complexity provides faster – smaller number of steps along channel – and more detailed information encoding about a subject. This view is supported by experimental results [44].

It is important to remind that there is redundant information about natural objects provided through different sensory modalities to the brain. For example, voices and faces both give information about the speech content, age, and gender of a person. Thanks to this redundancy, multimodal recognition is fast, robust, and automatic [65].

From the theoretical point of view it would be important to connect the function C_{IF} with Shannon information and capacity dimension of chaotic sets (see, for example [66]). However there are two principal steps that have to be addressed to build a bridge between the description of transient trajectories in heteroclinic channels and asymptotic dynamics on chaotic attractors: (i) it is necessary to introduce a specific measure (non-invariant), and (ii) to consider not continuous flows but maps.

To conclude this subsection we have to emphasize the important role that coherence phenomena can play for the cooperation of sensory information, which we did not considered here. More than twenty years ago, a very attractive neural synchronization hypothesis for the binding problem was formulated [67]. There are recent results supporting this hypothesis but it still needs further experimental testing [68] (see Fig. 10).

3.4. Flow stability – working memory capacity

The stability conditions of the models that we have discussed above provide us with a very powerful tool to address and predict several dynamical aspects of brain activity. In particular, we can calculate how long a typical heteroclinic channel can be, i.e., how many steps the sequential switching can have. Let us consider here the example of how to use this approach to find the origin of the limited capacity of working memory [69].

Working memory (WM) is the ability to transiently hold in mind and manipulate several items that are involved in a given information processing or actions such as thinking, planning or producing a motor output. Tasks involving WM include, for example, remembering a sequence of statements that we recently heard in a speech or following directions to an unknown place. Language, as a sequential activity, is also based on WM. However, the capacity of WM is limited and this is one of the reasons why the metaphorical term blackboard of the mind has become popular to describe WM.

The capacity of sequential WM is defined as the number of items that can be recalled correctly after a WM task, and varies amongst different individuals, depending also on age and health conditions. Numerous studies have led to the generally accepted view that the effective capacity for healthy subjects ranges between three to seven items [70–73]. This limit has coined the term magical number seven [74] in conjunction with WM. In fact, this number is not strictly seven, but something in the range 3–7 depending on the subject.

Information processing related to WM activity can be represented in an abstract space (the phase space of the network that implements the working memory) as a continuous flow of liquid phase: the incoming information encoded in a spatiotemporal manner excites the specific network with a functional reverberate loop that sustains the corresponding information item for a finite time (based on a transient attractor). The item networks are inhibitory interconnected with each other and build a macroscopic network that keeps the whole sequence of items. The cooperative dynamics of this macro-network can be based on the WLC principle and guarantee that the sequential items are recalled in the right order. Thus, all three processes – storing, maintaining and retrieving of sequential information, in fact, can be thought as continuous transient dynamical activity of hierarchically organized functional neuronal networks [49]. This perspective has also been discussed in another model based on an echo state network [75].

As many experiments show (see for a review [76]), functional inhibition is reflected in oscillatory activity in the brain at the frequency band of 8–13 Hz (alpha rhythm). The alpha activity can facilitate sequential inhibition by reducing the activity of a given network. There are several models of WM based on the idea that all steps of WM information processing in the engaged distributed networks is reflected by neuronal synchronization in the gamma band (30–80 Hz) accompanied by a theta (5–8 Hz) or an alpha band [77–80]. It is reasonable to hypothesize that such synchronization leads to a temporal coordination between the fast one-item processing and the slow sequential item interaction. One can expect that this coordination supports the robustness of information processing and contributes to a larger WM capacity [81]. Now we show that sequential WM capacity in the context of our model is limited by conditions of the retrieval process stability [69].

The dynamical model for sequential WM that we would like to discuss here is based on WLC between informational items [69]. These items are represented in the phase space by saddle fixed points and the mnemonic recall by a trajectory in a stable heteroclinic channel (SHC) [20,31]. In contrast to attractor dynamics, the transient itself reflects the sequential memory. Under certain simplifying assumptions, there is an upper bound on the number of items that can be stored in this sequential WM model when implemented by inhibitory-coupled neuronal clusters. Dynamics of such information items can be described by the generalized Lotka–Volterra model (2). In the case of a single family modality, i.e., $M = 1$ we have the traditional Lotka–Volterra model. One of the remarkable features of this model is the existence in the phase space (for a wide range of control parameters) of a stable heteroclinic channel that corresponds to robust sequential switching from one metastable state to other [82,52,20].

The authors of [69] assumed that the relative connection strengths are sampled from uniform distributions and cannot exceed an order of magnitude. They found that the bound for the number of items is about seven. This is remarkable because, the model dynamics exhibit the very same inherent bound for sequential WM capacity as given by the magical number. Let us briefly explain this result. Sequential WM dynamics is separated into two stages: the storage of sensory information and its retrieval. Storage means initiation of a specific pattern in the phase space of the corresponding dynamical system by both sensory input and the contents of WM. Based on the hypothesis that WLC between different informational items is the main mechanism for the correct retrieval in sequential WM, the authors in [52] have analyzed the structural stability of sequential switching, i.e., the correct reproducibility of the sequence of the informational items (which is the key property for memory performance). The stability conditions require a strong enough inhibition in the WM random network and, what is a key point, the level of the inhibition increases exponentially with the WM capacity. If we suppose that the ratio between the level of external inhibition and the self inhibition ρ_{ij}/ρ_{ii} is about 20 (large enough from the neurobiological point of view), the number of successfully recalled informational items, according to the exponential law, has to be between seven and eight (see

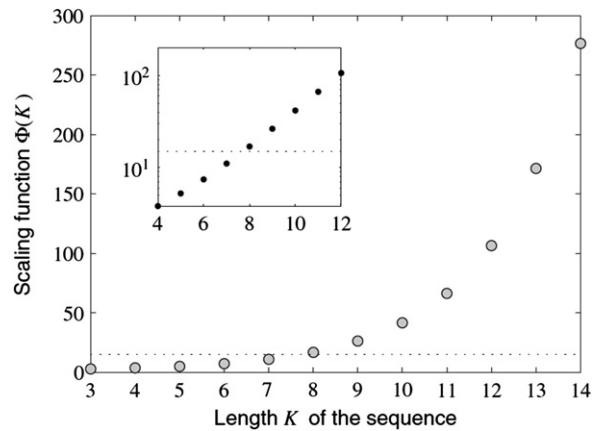


Fig. 11. Dependence of sequential memory capacity on the normalized level of network inhibition $\Phi(K) = \rho_{ij}/\rho_{ii}$ (adapted from [69]).

Fig. 11). Recently, a functional magnetic resonance imaging (fMRI) study [70] has provided experimental evidence for the dependence of the capacity limitation for visual WM on the level of inhibition.

WM capacity depends on both the environment information and the memory information. In our case, this is reflected in the mode's architecture through subject and external information dependent parameters, i.e., connection strengths that represent lateral inhibition. In particular, the dependence on the individual has to be emphasized, since it modulates how external information actually changes the parameters themselves. For example, cognitive control plays a role in the individual perception of a painful stimulus because it determines how the external information is translated into functional networks. Therefore, individual traits can modulate the subjective experience, leading to a subject dependent experience of the same external information. If we assume a relationship between the level of pain and inhibition, the suggested model can be used to predict the dependence of working memory capacity in the presence of pain [49].

With binding WM capacity can be higher. Thus, working memory capacity depends on the environment information, memory information and multisensory binding.

3.5. Flow instability – dynamical origin of mental disorders

The human brain forms functionally dependent networks of specific interconnected brain regions that together are responsible for both the cognitive and emotive activity of the person. The instability of the information flows that characterize the dynamics of such networks is reflected in a non-normal behavior or, in clinical cases, in psychiatric disorders. We present here two examples of such instabilities that are related to obsessive–compulsive disorder (OCD) and bipolar disorder (BD).

The OCD is a type of an anxiety disorder that traps people in endless cycles of repetitive feelings, unwanted thoughts and unwanted repetitive acts which the sufferer realizes are undesirable but is unable to resist – compulsive rituals. The compulsive rituals characteristic of OCD are performed in an attempt to prevent the obsessive thoughts or make them go away. Although the ritualistic behavior may make the anxiety go away temporarily, the person must perform the ritualistic behavior again when the obsessive thoughts return. People with OCD may be aware that their obsessions and compulsions are senseless or unrealistic, but they cannot stop themselves. Fig. 12 represents the interrelation in the phase space of different information flows corresponding to cognitive and emotive activities that characterize the OCD. The flow (A) describes four steps (metastable states, represented by green balls) of the normal behavior of writing with a pencil (i.e. picking up the pencil, carrying it to the piece of paper, placing it on the paper, etc.) leading to final completion of the activity denoted by the red ball. However, in the case of someone with OCD, at the fourth step the person may suddenly realize that the pen is contaminated and interrupt the behavior in order to wash his hands (SHC R – ritual – consisting of five additional steps such as picking up the soap, turning on the water, etc.). In the case of OCD, at completion of R the behavior may not return to the original state A and instead could exit into several other possible flows representing different degrees of impairment dictated by the emotion–cognitive appraisal of the situation. For example, in case (B) the person could pick up the pencil and at the second step realize

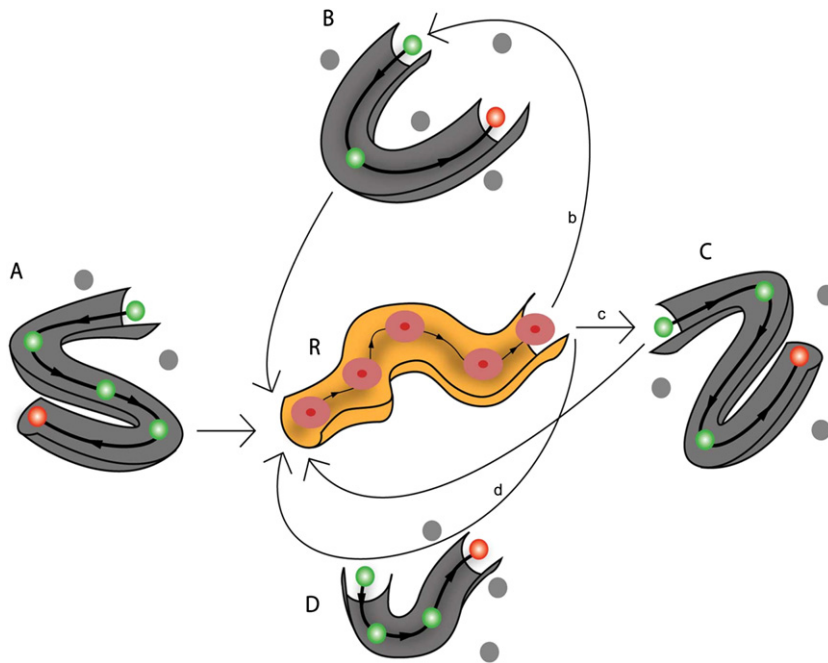


Fig. 12. Interrelation in the phase space of different information flows corresponding to cognitive and emotive activities that characterize the OCD. Gray balls represent metastable states in cognitive–emotion phase space that did not become active. See description in the text (adapted from [83]). (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

that the pencil is still dirty and go back to the ritual of washing (flow R). In the example of flow (C) the person may have touched the pen and immediately returns to ritual (R). Flow (D) represents a state in which the person with OCD, once his symptoms are triggered, stays in the ritual without going back to the contaminated pencil until the resources are exhausted or some other factors come into play.

The mathematical model discussed above in the form of kinetic equations that represent the interaction of different cognitive and emotion modes permits to describe other anxiety disorders such as panic or bipolar disorder [83]. To understand the instability that leads to bipolar disorder in the framework of a general model, we have to specify the competitive mental modes. This can be done by employing several different modes that represent a specific cognitive activity, for example, decision-making, utilizing short-term memory, and attention. The next step is to specify three emotion modes that represent normal mood (mode N), depression (D) and euphoria (E). Normal subjects and bipolar patients will demonstrate different types of behavior, i.e., different dynamics that are projected to different areas of the parameter space that are separated by bifurcation boundaries. The transition through such boundary translates to the emergence of a new instability and new dynamics. Computer modeling of the general model with six modes has demonstrated the existence of chaotic sequential switching between D and E with random time intervals between them. This corresponds to bipolar disorder presentation dynamics. The mathematical image of such dynamics is a strange attractor and the corresponding time series looks like: ...NDNNENDDDNEENDNENNDNNE... Similar data has been recently reported in [84] where the dynamics of mood switching in a bipolar disorder for mania and depression episodes (see Fig. 13).

4. Information flow between brains

4.1. Speaker–listener information flow: sequence of informational units

Here we want to consider the problem of information transduction by language from one brain to other – a speaker–listener problem – based on a dynamical point of view. It is well known that in a real world context, language contains much more information than just a formal message, such as information about the speaker, for example about his social background, his emotional state of mind, and, in general, his cognitive features (see [85]). To represent a speaker–

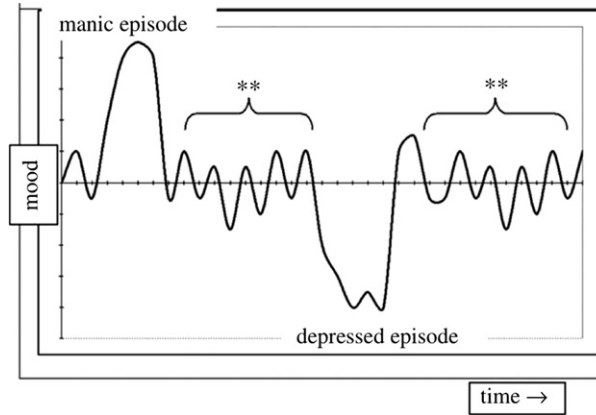


Fig. 13. A schematic of mood patterns in bipolar disorder: the disorder does not simply feature full blown episodes of mania and depression with periods of normality. Rather, ongoing inter-episodic mood instability is also a clinically common, yet a poorly understood feature of the disorder. The beginning of mood instability is marked by double asterisks (adapted from [84]).

listener problem in a dynamical way we have to introduce informational items that do not necessarily coincide with words.

Language is organized hierarchically [86]. Words, which are themselves collections of phonemes, make up sentences, which again make up paragraphs or other larger collections of information. In this hierarchy, sequential ordering plays a prominent role since it is an essential part of the semantic and syntactic structure. Rather than talking about words in a classical sense, we should consider ‘informational units.’ A sequential order of these informational units then constitutes an informational sentence, i.e., the shortest form of a message. Messages usually consist of several such sentences. How can these informational units – we will also refer to them as ‘linguistic modes’ – be interpreted? In our context they can be seen as entities that carry semantic information such as things like ‘red apple’ or ‘table’ and relations thereof ‘on the,’ which can relate two or more objects. These informational units combined give the informational sentence ‘red apple on the table.’ Although intermediate levels of combining information are present in natural language (e.g., ‘chunking,’ phrases, relative clauses), we want to restrict ourselves here to two levels in the hierarchy, one to describe informational units and a second for informational sentences as sequences of informational units.

Suppose the speaker wants to convey a message. He then has to decompose the message into informational sentences which themselves consist of informational units. A sequence of informational units is uttered as a sequence of phonetic words to the listener. The listener now has to interpret this sequence of phonetic words to extract the message. His brain has to be capable of interpreting the (language dependent) phonetic words to recover the informational units while doing an online integration to reconstruct the informational sentences and finally the message itself (see Fig. 14). Thus, the dynamical model can consist of two unidirectionally coupled dynamical systems, one for the speaker, and one for the listener. Each of these systems consists of coupled dynamical systems with distinct time scales representing the different levels in the hierarchy. Informational units and informational sentences are represented by saddle sets in the phase space of the system corresponding to the level in the hierarchy. Temporal relations in the form of sequential ordering can be realized as heteroclinic connections between these saddle sets (SHCs). Through the hierarchy, sequences of informational units will be identified with an informational sentence.

The dynamical system that we are looking for can be described by the following set of differential equations. Let Q denote the message to be transmitted. We will call R to the activity of the speaker’s informational units and V to the activity of the informational sentences. The speaker’s dynamics are given by

$$\tau_R \frac{dR_j}{dt} = R_j \left(\alpha_j(Q, V) - \sum_{k=1}^M \beta_{jk}(Q, V) R_k \right) \quad (7)$$

$$\tau_V \frac{dV_i}{dt} = V_i \left(\gamma_i(R) - \sum_{k=0}^N \delta_{ik}(R) V_k \right) \quad (8)$$

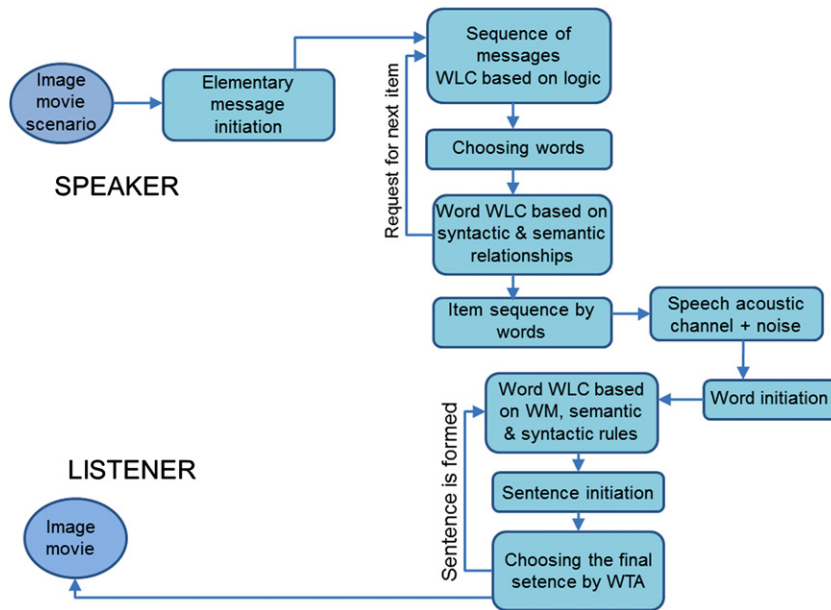


Fig. 14. Schematic of message transduction. Here for simplicity we name the informational units as words.

where $j = 1, \dots, M$ and $i = 0, \dots, N$. The dependency of the parameters on the dynamical variables will be described below. With \tilde{V} being the distorted sequence of words uttered by the speaker, the listener's dynamics are described by

$$\tau_W \frac{dW_i}{dt} = W_i \left(\theta_i(\tilde{V}, S) - \sum_{k=0}^{N'} l_{ik}(\tilde{V}, S) W_j \right) \quad (9)$$

$$\tau_S \frac{dS_j}{dt} = S_j \left(\kappa_j(W) - \sum_{k=1}^{M'} \lambda_{jk}(W) S_k \right) \quad (10)$$

where $i = 0, \dots, N$ and $j = 1, \dots, M$. Correspondingly, W and S stand for the activity of the listener's informational units and sentences. All parameters denoted by lowercase Greek letters have positive, real values and $\tau_V < \tau_R$, $\tau_W < \tau_S$ denote the timescales.

The speaker's dynamics are closely related to the concept of hierarchically coupled heteroclinic channels as proposed in [87] (see Fig. 14). When the speaker initiates the transduction of a message, the formation of informational sentences corresponds to the formation of a stable heteroclinic channel in the topmost level of the speaker's dynamical system. Due to the nature of the channel, the dynamics will follow the heteroclinic sequence, leading to sequential activity of the nodes corresponding to the informational sentences. While an informational sentence is active, it imposes a stable heteroclinic sequence on the lower level, which corresponds to the temporally ordered sequence of informational units. The result is a sequence of sequences of informational units that is uttered to the listener in form of a sequence of phonetic words in a specific language. It is important to emphasize the difference between a sequence of informational units and a sequence of phonetic words in a language: a sequence of informational units is a temporal, logically sound sequence of semantic units whereas a sequence of phonetic words is a grammatical sentence in a language. Furthermore, some of the information in the sequence of informational units will not necessarily be contained in the sequence of phonetic words but might result in a change of prosody, e.g., different stress patterns, or other mechanisms that carry semantic information.

The uttered words will reach the listener through a noisy channel. The listener has to use his own lexicon of informational units and sentences to recover the message. Note that such a lexicon is different and complimentary to a lexicon of phonetic words. We suggest that the mechanism for this reconstruction is competitive interaction in a non-autonomous dynamical system which is driven by the input provided by the speaker. This is in contrast to probabilistic models that have been proposed before and it is important to emphasize here the principal differences of a dynamic

approach versus the traditional structured probabilistic approaches to semantic cognition (see, for example [88]). The task of the listener is not just to discriminate between predefined structures but learning should ideally also enable the addition of new, previously unknown items through a dynamical process. Input by a speaker's informational unit will activate a subset of the listener's informational units, namely the units that are similar. The resulting sequence of informational sentences then corresponds to the message that was received by the listener.

Let us illustrate the above by giving an example. Imagine we want to tell the fairy tale *Three Little Pigs* [89] to our grandson. The first step of telling the story is to sequence it into sentences, for example:

The three little pigs built their new houses.
 The first pig built his house out of straw.
 The second pig built his house out of sticks.
 The third pig built his house out of bricks.
 The wolf huffed and puffed and blew the straw house down.
 The wolf huffed and puffed and blew the stick house down.
 The wolf huffed and puffed but couldn't blow the third house down.
 The wolf ran to the woods and never came back again.

Every one of these sentences now contains various informational units. The second sentence, for example contains the items first pig, house, and straw and the verb built relates those three items. Note that informational units are difficult to define, and our suggestion in this example depends on intuition. The result of the sequencing process is a sequence of sequences of informational units. It is important to note the similarities between the model of message transduction and the working memory that we discussed above. In fact, it is well accepted that working memory plays a key role in language processing. For our model, working memory can be seen as a key ingredient; an informational sentence imposes a stable heteroclinic channel on the word level. This can be interpreted as a sequence of items being loaded into working memory. Correspondingly, the message itself is such a sequence of informational sentences, which are active in working memory. A restriction on the number of items that can be held in working memory, which comes from the conditions on the existence of a stable heteroclinic channel now corresponds to a restriction of the number of informational units that a message can contain in our language model. In other words, our model predicts a maximum number of informational units and informational sentences that a message will be split up into by the speaker.

The situation is a bit more subtle for the listener's dynamics. If we assume that the input by the speaker not only activates the corresponding informational units and sentences but also leads to an active formation of a stable heteroclinic sequence in the phase space of the listener's dynamical system, then the results for working memory also carry over to the listener's dynamics. In fact, such an assumption is not unreasonable, because if such a structure in the phase space is not built up, a recall of the information that was just processed would be impossible. Being able to recall, however, should be one feature of understanding the message.

The limit of informational units, which is induced by limited working memory capacity, is a limit on abstraction representations of information. How can such a limitation be quantified in the context of natural language processing? It is wrong to assume that such a limit will just translate to a limit of the number of words in a sentence, since words and informational units are usually not in a directly corresponding one-to-one relationship. If one had a (language-dependent) estimation of the average number of words per informational unit, this would result in an average limit of the number of words, depending on the language. Thus, the question that we have to address is more general: How can one quantify the number of informational units that are present in a sentence in natural language? Semantic complexity measures [90] could provide a way to measure the amount of information that is present in natural language. Moreover, there are approaches which relate language and working memory through cognitive load theory [91] that has mostly been used for instructional purposes. Based on this theory, bounds for the length of optimally understandable sentences were investigated [92].

The model we proposed gives rise to additional mathematical challenges. The restrictions that working memory imposes for the speaker carry over only when there is a unidirectional coupling. For the listener, a feedback connection leads to the desirable feature of anticipation, but also the speaker's dynamics feedback could lead to the accommodation of sentences of different lengths. Recurrently interacting heteroclinic dynamics, however, are still poorly studied.

Moreover, the learning rule to generate the input-dependent heteroclinic channel in the phase space of the listener's dynamical system has yet to be formulated, a necessity for the developing of the theory and its applications.

4.2. *Information exchange between brains. Brain synchronization*

When people interact, affective information is transmitted between their brains. Everybody can recall the pain that we get looking at the face of another person receiving a painful stimulus. Anders et al. have investigated the dynamics of brain-to-brain transfer of affective information [93]. They used information-based functional magnetic resonance imaging (fMRI) to investigate the flow of affective information between the brains of senders and perceivers engaged in ongoing facial communication of affect. It has been found that the level of neural activity within a distributed network of the perceiver's brain can be successfully predicted from the neural activity in the same network in the sender's brain, depending on the affect. They also investigated the sequential dynamics of the information exchange – whether early information from the sender's brain was encoded early in the perceiver's brain, and late information from the sender's brain was encoded later in the perceiver's brain. The data show that affect-specific information is encoded in a very similar way in the brains of senders and perceivers engaged in facial communication of affect. Information is successively transferred from the sender's brain to the perceiver's brain, eventually leading to what has been called a shared space of affect [94].

An interesting brain interaction phenomenon – brain synchronization was investigated recently. Suppose two participants are doing joint social job and both are continuously active. Each of them is modifying his/her own actions in response to the continuously changing actions of the partner. This continuous mutual adaptation results in interactional synchrony to which both members contribute. How does the participant's brain activity underlie this process? Dumas et al. are trying to answer this question using hyperscanning recordings – simultaneous recording of the hemodynamic or neuroelectric activities of multiple subjects [95]. It remains largely unknown to what extent oscillatory synchronization could emerge between two brains during social interaction. The authors have discovered that states of interactional synchrony correlate with the emergence of an inter-brain synchronizing network in the alpha–mu band between the right centro-parietal regions. These regions have been suggested to play a pivotal role in social interaction – they acted symmetrically as key functional hubs in the interindividual brain web. Additionally, neural synchronization became asymmetrical in the higher frequency bands possibly reflecting a top-down modulation of the roles of model and imitator in the ongoing interaction.

5. Discussion

Modern cognitive science describes cognitive activity of human and animals as embodied, goal-situated information dynamics, emergent from the interaction of the brain, the body and the material and social environment. Thus, brain information flows between sensory and behavioral units are induced by functionally top-down feedbacks. Analyses of such information flows in brain (physical) space are very constructive for the understanding of brain unit interaction and help to illuminate the specific role of various subsystems on the generation of behavior in normal and pathological situations [43,96].

The human brain operates, however, with highly interconnected functional networks whose activity is constantly changing in time and can be represented as global mode interactions [97–99]. In order to understand the dynamics of global information flows, we introduced here the notion of information flows in the phase space of the dynamical system that describe the global mode interaction and its evolution in time. Such approach gives a unique possibility to investigate key cognitive problems as stability (robustness) of cognitive information flows and the interpretation of associated instabilities. We argue that different psychiatric disorders can be described by different kind of cognitive information flows instabilities [83]. For example a chaotic instability can be used to describe a bipolar disorder [84].

Based on information flow stability analyses, we have provided an explanation of why working memory (short-time memory) capacity cannot be larger than 5 ± 2 information items. We have also discussed theoretical results that indicate that object recognition based on multimodal sensory information can be several times faster if the system is able to integrate information about different features (binding process) on the perceptual level.

Concluding this review we wish to emphasize one of the key problems that hopefully will be solved soon: the construction of dynamical models that can describe global information flows in the brain directly from experimental data. Multielectrode recordings and high-resolution neuroimaging techniques generate multivariate data that are the

basis for understanding global pattern interactions [100]. How to extract the dynamical characteristics of information flows from these data is a challenge that can be addressed with the approaches that we have reviewed in this paper.

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