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## Neuroscience and architecture

*modulating behavior through sensorimotor responses to the built environment*

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*Published in:*  
Neuroscience & Biobehavioral Reviews

*DOI (link to publication from Publisher):*  
[10.1016/j.neubiorev.2022.104715](https://doi.org/10.1016/j.neubiorev.2022.104715)

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*Publication date:*  
2022

*Document Version*  
Publisher's PDF, also known as Version of record

[Link to publication from Aalborg University](#)

*Citation for published version (APA):*  
Djebbara, Z., Jensen, O. B., Parada, F. J., & Gramann, K. (2022). Neuroscience and architecture: modulating behavior through sensorimotor responses to the built environment. *Neuroscience & Biobehavioral Reviews*, 138, [104715]. <https://doi.org/10.1016/j.neubiorev.2022.104715>

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## Review article

## Neuroscience and architecture: Modulating behavior through sensorimotor responses to the built environment

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## ARTICLE INFO

## Keywords:

Thalamus  
Pulvinar  
Exogenous attention  
Environmental feature  
Sensorimotor feature  
Neuroarchitecture

## ABSTRACT

As we move through the world, natural and built environments implicitly guide behavior by appealing to certain sensory and motor dynamics. This process can be motivated by automatic attention to environmental features that resonate with specific sensorimotor responses. This review aims at providing a psychological framework describing how environmental features can lead to automated sensorimotor responses through defined neurophysiological mechanisms underlying attention. Through the use of automated processes in subsets of cortical structures, the goal of this framework is to describe on a neuronal level the functional link between the designed environment and sensorimotor responses. By distinguishing between environmental features and sensorimotor responses we elaborate on how automatic behavior employs the environment for sensorimotor adaptation. This is realized through a thalamo-cortical network integrating environmental features with motor aspects of behavior. We highlight the underlying transthalamic transmission from an Enactive and predictive perspective and review recent studies that effectively modulated behavior by systematically manipulating environmental features. We end by suggesting a promising combination of neuroimaging and computational analysis for future studies.

## 1. Introduction

During our daily interaction with the environment, we are constantly and automatically adapting behavior according to the features of the environment that evoke exogenous attention. As opposed to endogenous attention, exogenous attention is an involuntary, automatic, and stimulus-driven component of spatial attention (Carrasco, 2011). And even if such automated behavioral adaptations to the environment, like automatically adapting our gait according to the various pavements encountered in the city, happen countless every day, the functional coupling between *environmental features* (EFs; features pertaining to the environment) and associated *sensorimotor responses* (SMRs; responses pertaining to cortical and bodily processes) that underlie such automated behaviors remain poorly understood. Most of the time, we are not explicitly aware of the built environment that consequently acts as a backdrop to other ongoing everyday tasks. Although a walk through the city overwhelms sensory systems by diverse behaviorally-important sensations (e.g., changes in terrain, corners, other people, and so on),

we usually become aware of only a fraction of these. The built environment thus affects us through automatic, exogenous visual attention to EFs that often escape awareness, i.e. attention without (perceptual) awareness (Dehaene et al., 2001; Vuilleumier et al., 2001; Moutoussis and Zeki, 2002; Marois, Yi and Chun, 2004; Sergent, Baillet and Dehaene, 2005). Making automatic use of EFs to guide behavior is an important frugal capacity of the human brain and body given the limited energy available and the cost of neuronal activity when it enhances selected signals through voluntary, endogenous attention (Lennie, 2003; Clark, 2015).

Visual attention corresponds to the gain of specific visual signals (McAdams and Maunsell, 1999; Reynolds, Pasternak and Desimone, 2000; Martínez-Trujillo and Treue, 2002; Carrasco, Ling and Read, 2004) and can be achieved by two distinct attentional orientation types, namely *covert* and *overt* attention (Posner, Snyder and Davidson, 1980; Carrasco, 2011; Maunsell, 2015). Overt attention is characterized by shifting our gaze onto the object of interest, whereas covert attention is the shift of attention without moving the eyes, i.e. enhanced peripheral

**Abbreviations:** EFs, Environmental Features; SMRs, Sensorimotor Responses; SMC, Sensorimotor Contingency; INT, Intrinsic Neural Timescale; MoBI, Mobile Brain/Body Imaging; FO, First-Order; HO, Higher-Order.

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<https://doi.org/10.1016/j.neubiorev.2022.104715>

Received 29 March 2022; Received in revised form 23 May 2022; Accepted 25 May 2022

Available online 30 May 2022

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vision (for review, see: Anton-Erxleben and Carrasco, 2013). Adding *endogenous* and *exogenous* to the two covert and overt attentional orientation types describes whether the reorientation was voluntary (e.g., the exogenous shift from overt to covert) or not (e.g., endogenous shift from overt to covert). However, in this paper, as both covert and overt attention enhance sensory signals, we focus particularly on how exogenous attention is used to facilitate behavioral adjustments. Note the distinction between *awareness* and *attention*; we can be attentive to specific EFs without being aware of them, but we cannot be aware of specific EFs without paying attention to them (Dehaene et al., 2006; but see; Phillips and Block, 2017). Furthermore, as intrinsic neural time-scales have been demonstrated to be of significant importance when considering the organization of the brain (Golesorkhi, Gomez-Pilar, Tumati et al., 2021; Golesorkhi, Gomez-Pilar, Zilio et al., 2021; Wolff et al., 2022), we consider the relationship between SMRs and EFs to be of fast INT in nature, as opposed to longer INTs displayed by the default mode network.

EFs modulate behavior by biasing the execution of SMRs that are associated with distinct behaviors (Palmer and Kristan, 2011; Romo, Lemus and de Lafuente, 2012; Khan and Hofer, 2018). For instance, while driving on the highway, decreasing the distance between the white lines that mark the lane causes us to slow down because rapid changes in sensory signals relative to our movement are associated with increased velocity. Here, the EF corresponds to the white lines marking the lane whereas the SMR corresponds to the sensed changes relative to the performed (constant) movement and subsequent slowing down. Although a specific EF is typically associated with a preferential SMR, this distinction is practical as it allows us to distinguish between agent and environment. As we will demonstrate, this EF-SMR relation is based on early thalamocortical activity that influences how optic flow in primary visual areas of the brain is processed relative to bodily action. This is different from self-motion studies that modulate the environment based on digitally amplified optic flows in virtual environments compared to walking speed (Prokop, Schubert and Berger, 1997; Bremmer and Lappe, 1999; Mohler et al., 2004; Banton et al., 2005; Lamontagne et al., 2007; Chaplin and Margrie, 2020). Environmental modulation is instead based on feature changes that either occurs naturally or that are man-made, (i.e., designed), so that SMRs automatically continue to invoke specific behaviors as part of a network of possible actions through active predictions (we will elaborate on the network in Section 3.1, but first we will clarify what we mean by predictions). The use of predictive processes to understand attention, sensory, and motor processes has been widely embraced in a variety of psychobiological frameworks and has been growing given its biological plausibility (Elman, 1990; Mumford, 1992; Dayan et al., 1995; Rao and Ballard, 1999; Friston, 2005; Friston and Kiebel, 2009; Itti and Baldi, 2009; Clark, 2015; Friston et al., 2017).

This paper aims to bridge SMRs with predictive neurophysiological processes of attention to expose how designed EFs affect the neural substrate of meaningful experiences. Based on a psychobiological framework, we propose an approach for investigating such processes empirically. We see this as an important step towards better understanding how and which features of the environment can help enhance the sensorimotor processes relevant to typical and divergent brain/body states. Identifying the underlying brain systems that partake in the neurobehavioral mechanisms underlying adaptive behavior allows, through the combination of data-driven and hypothesis-driven analyses, for measuring processes that are not readily observable in everyday behavior.

The structure of the paper is as follows. Section 2 unpacks the definition of SMRs through a psychobiological framework concerning the action-perception loop that draws on Enactivism and a predictive view of the brain. We briefly introduce the thalamus as a central subcortical structure to suggest that the brain does not rely on incoming sensory signals alone (Sherman and Guillery, 1996, 2002; Sherman et al., 2015), but more on its integrative and predictive capacity giving it a frugal advantage<sup>1</sup> (Barrett and Bar, 2009; Friston, 2010; R. Adams, Shipp and Friston, 2013; R.A. Adams, Shipp and Friston, 2013; Seth, 2014). Predictive neuronal dynamics are leveraged to establish the importance of environmental change and self-motion in transthalamic transmission in the pulvinar and multiple cortical regions critical for cognition and behavior. This essentially leads us to propose a neuronal scheme of how SMRs, based on exogenous attention, enable automatic adaptive behavior. It is by tying SMRs with predictive capacities and transthalamic transmission that the associated EFs can affect cognition and behavior. In Section 3, we discuss EFs and SMRs and focus on how sensory responses when interacting with a specific EF can give rise to distinct motor behaviors through top-down predictions. As the sensory responses are associated with a repertoire of specific motor behaviors mapped throughout a network of actions that can be automatically invoked through attentional influences, we suggest that minimal environmental changes could give rise to very distinct SMRs.

In Section 4, we provide evidence for our perspective. We first demonstrate that urban structures, i.e. EFs, that are staged by designers, inherit specific SMRs through planned rectangular grids and natural unplanned districts. We further support our perspective by reviewing studies that extend from behavioral observations to intracranial neurophysiological studies demonstrating that distinct SMRs affect cognition and behavior in distinct and automated ways. Finally, in Section 5, we suggest that Mobile Brain/Body Imaging (MoBi; Makeig et al., 2009; Gramann et al., 2011, 2014) applied to human beings in combination with generative and causal modeling qualifies as an excellent candidate for future studies. This approach can, for instance, investigate in a data- and hypothesis-driven manner which cortical areas are involved in automatic behavior as well as quantify how much the EFs affect neural dynamics.

## 2. Sensorimotor responses

### 2.1. Enactive neuroscience

What are sensorimotor responses? Not to be confused with the ongoing, continuous sensorimotor coordination when interacting with the environment, SMRs refer to a particular dynamic response to, or resonance with, an environmental feature and not just the extensive environment. As sensorimotor coordination refers to the ongoing coupling between sensation and motor behaviors in the environment it is temporally extended in contrast to an automatic adaptation, which is essentially a sensorimotor response. SMRs refer thus to rather preferential resonances with the environment as opposed to non-specific and ongoing coordination. Although there is much knowledge about sensory and motor systems themselves, our psychobiological framework uses principles of the built environment to understand how it impacts the functioning and organization of the human brain, changing our understanding of *action-perception loops*. The built environment can be thought of as not only the terrain on which cognitive acts (i.e., remembering, judging, planning, deciding, etc.) and other behavior-relevant processes unfold but as an important constitutive component of those acts and

<sup>1</sup> Although we take a predictive angle to understand the relations between EFs and SMRs, there are other alternative approaches, e.g. the temporo-spatial theory of consciousness (TTC; Northoff and Huang, 2017; Northoff, 2018), which may be more suitable in understanding the temporal dynamics of the relations in question.

processes. This idea challenges the traditional understanding of cognition and behavior, which is thought to be a passive sequence from sensory inputs to motor outputs. Instead, this idea champions a more contextualized and biogenic view; an interactive and dynamic relationship between sensory and motor processes in a given environment. This view emerges from the 4E-cognition (embodied, extended, embedded, and Enactive) perspective (Gallagher, 2017; Newen, De Bruin and Gallagher, 2018).

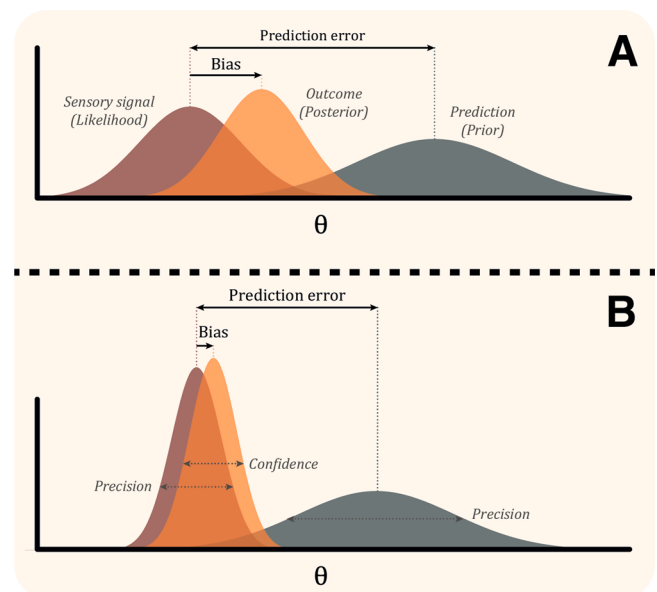
4E-cognition states that brains and their function cannot be understood separated from the bodies and environments they inhabit, offering a biogenic and grounded definition of cognition (Barsalou, 2008; Varela, Thompson and Rosch, 2016; Newen, De Bruin and Gallagher, 2018). Therefore, action-perception loops summarized under the umbrella term of *cognition*, are a direct product of the dynamic interaction between the brain/body/environment system. The critical insight is that human cognition and behavior are embodied and embedded processes produced by, and producing, movement. The roots of 4E-cognition rest on a life-mind continuity by appealing to autopoiesis (Thompson, 2007; Varela, Thompson and Rosch, 2016). Autopoiesis, a property of the organization of living systems, is a set of self-organizing principles that involve actively self-constructing system components and self-referencing by operational closure and thereby distinguishing between the living organism and its environment. The continuity coarsely corresponds to the dependence on biological processes necessary to life in the emergence of any mind-related capacity of the organism,<sup>2</sup> hence the psychobiological dimension. Consequently, as any living organism enacts a homeostatic balance governed by autopoiesis, it has a basic form of behavior and cognition (Varela, Maturana and Uribe, 1974; Maturana and Varela, 1992; Damasio, 2010). As a result, in the case of the sophisticated human organism, this view is positioning the built environment as a spontaneous and constitutive (or at least *enabling*) component of the cognitive act, ultimately tying human made environments with cognitive neuroscience (De Jaegher, Di Paolo and Gallagher, 2010; Rojas-Líbano and Parada, 2020).

Enacting our capacities means making use of the reciprocity in the central nervous system of action and sensation (Thompson and Varela, 2001; Thompson, 2005, 2007). It is precisely this practical attitude of the nervous system that allows cognition and behavior to emerge *in* and *from* the environment. It speaks to the dynamic relationship between sensation and action—both monitored by the embedded operation of the brain/body system. Among theories in embodied cognition, the theory of sensorimotor contingencies (SMC; O'Regan and Noë, 2001b, 2001a) proposes that cognitive skills are based on covarying sensations and actions bound by lawful changes in enacting perception. By starting from action, SMC claims that perception emerges from an active type of “knowing-how” rather than of “knowing-that” (Ryle, 1945) assuming that one knows how actions would change sensations so that a specific perception results. Notice that *perception* is here considered to be the active resonance with the surroundings, as opposed to *senses* as physiological processes. Concerning attention in visual perception, the experience of presence of our surrounding context even beyond peripheral vision is based on exercising the lawful changes in “knowing how” to move the body and eyes to reveal the predictable contextual sensory information. In other words, knowing the action that can successfully bring into view the predicted sensation is what constitutes our wholesome grip on the environment. In terms of predictive coding, this corresponds to the capacity to increase our sensory precision by moving in predicted ways.

<sup>2</sup> Over the course of time, different Enactive views of cognition emerged. ‘Autopoietic Enactivism’ is thus different from ‘Radical Enactive Cognition’ and from ‘Sensorimotor Enactivism.’ We rely on the forthcoming chapters on sensorimotor contingencies that are a form of Sensorimotor Enactivism.

## 2.2. Predictive neuronal dynamics

What could the underlying neuronal mechanisms of SMRs be? The predictive capacity provides one way to operationalize the aforementioned lawful changes throughout the body and brain as coupled to the environment, which is what we mean by Enactive inference, i.e. a predictive approach that recovers one of the critical components of the Enactive approach. Considering the visual system, the predictive capacity is based on sensory dynamics in hierarchically organized neurons (Rao and Ballard, 1999; Hochstein and Ahissar, 2002; Hohwy, 2013; Clark, 2015; Friston et al., 2017). Rather than passively responding to sensations, the perceptual system is actively engaged in generating predictions that propagate at different cortical layers. By constant monitoring of body physiology and states—such as heart, gut, proprioceptive, and vestibular dynamics (Blanke, 2012; Salomon et al., 2016; Richter et al., 2017) predictions in the hierarchy originate at the highest cortical level (Hochstein and Ahissar, 2002; Buffalo et al., 2010) providing downward (top-down) feedback relative to ascending (bottom-up) predictions errors. Thus, bottom-up signals that remain unfiltered by top-down propagation (i.e., prediction) are processed, suggesting that the embodied brain operates in a dynamic error-corrective fashion (Fig. 1). As evidence suggests, predictions are of a global nature (Bar et al., 2006; Campana et al., 2016). Hence, if the prediction of the “gist of the scene” does not encounter any errors through our sensory system, then there is nothing worth updating as the environment is predictable and such processes would require additional resources and processing steps. Notably, prediction errors are precision-weighted so that the level of correction is relative to the certainty of the sensory signal (Feldman and Friston, 2010; Brown et al., 2013). Certainty or confidence is inversely related to the variance of the



**Fig. 1.** Attention process based on (Bayes) optimal predictive processes in the visual system. A. The normal distributions illustrate the sensory signal as a function of a parameter (theta on the x-axis), the prediction, and the perceived outcome. The sensory signal designates what the sensory system is reporting, while the prediction designates what the system was expecting, and taken together, the outcome designates what passes through. B. The posterior outcome is affected almost equally by the prediction and the sensory signal. However, once the precision of the sensory signal improves (an increase of precision or decrease of uncertainty) so that the signals accumulate more around the mean, the posterior outcome is more biased by the sensory signal. This can be seen on the B-diagram. Although this bias is achieved by upregulating the sensory precision, the same bias can also be achieved by downregulating the precision of the prediction.

sensory signal meaning that high confidence corresponds to low variance, and vice versa (Feldman and Friston, 2010). Based on sensory and proprioceptive cues, sensorimotor dynamics emerge from the updating of either the sensory signal or the prediction thereof using their relative mean and precision to estimate the posterior outcome.

In computational terms, as this process unfolds, the prior predictions are updated to the posterior distribution by combining the sensory signal with the prediction. Adjusting the precision of either the sensory signal or the prediction can greatly affect the bias on the posterior outcome (Fig. 1). Practically, the adjustment occurs by either enhancing our predictions, i.e. increasing the precision/decreasing the uncertainty about what we believe we must perceive, which could lead to the experience of hallucinations (R. Adams et al., 2013; R.A. Adams et al., 2013), or by simply acting to gain additional sensory information that will increase sensory precision (Friston et al., 2017).

In the interest of attention, optimizing the precision of the signals in the visual system will lead to a stronger bias on the posterior outcome, which also affects the predictions when updated with the posterior distribution. Importantly, the increase of attention affects the neuronal hierarchy through post-synaptic gain that in turn enacts associated neuronal populations (Hillyard, Vogel and Luck, 1998; Jiang, Summerfield and Egner, 2013; Smout et al., 2019; Limanowski and Friston, 2020). Attention then is the optimization of signals in the visual system reflected in synaptic gain that can appeal to associated neuronal populations. Associations materialize when predictions about the signal are updated upwards using the posterior estimate to generate neuronal activities that are associated with the specific behavior. It is within this transition between prediction regimes (i.e., the enacted association) through the control of post-synaptic gain that we propose to cause an automatic environment-mediated modulation of behavior and cognition. As EFs affect sensory precision through attention, we now address the neurobiology of the pulvinar (thalamic nuclei) and visual cortex to better understand the integration of optical flow, environmental changes, and sensory confidence. As the following reveals, the integration depends on transthalamic transmission between cortical areas. This means that EFs appeal to behavior-related processes through early sensorimotor processes, which we refer to as SMRs.

### 2.3. Orders of thalamic nuclei

To contextualize the previous section, we focus on what happens when the sensed environment changes faster or slower than expected relative to self-motion. We commence from early sensory processing in subcortical structures and then move on to the role of optical flow in cognition in general. Early sensory processing involves thalamic nuclei, which for a long time was considered a passive relay station of sensory information to the cortex<sup>3</sup> with virtually no active role in cognitive functions. However, studies provide accumulating evidence that nuclei in the thalamus form integral loops with cortical areas relevant to numerous cognitive functions (Sherman and Guillery, 2011, 2013; Ward, 2013). Accordingly, the thalamus is vital for both synchronizing cortical activity across brain regions, as well as regulating cortical excitability, rendering the thalamus as actively engaged in the continuous processing of information between cortical areas (Mitchell, 2015; Halassa and Kastner, 2017; Kastner, Fiebelkorn and Eradath, 2020). This means that transthalamic pathways can operate in parallel to cortico-cortical sensory processing where thalamic neurons can transform information in important ways.

The thalamus is constituted by several nuclei, i.e. clusters of neurons with similar functions, that can be segregated into either first or higher-order nuclei. The orders describe their origin of inputs. *First-order* (FO) nuclei are the first to relay the sensory information, e.g. lateral geniculate nucleus (LGN) for the visual system, to the cortex, whereas *higher-*

*order* (HO) nuclei, e.g. the pulvinar for the visual system, receive their driver input from the cortex (Shipp, 2003; Sherman and Guillery, 2011, 2013; Halassa and Kastner, 2017). This practically means that once FO thalamic nuclei have transmitted information to the cortex it is then driven back to a HO thalamic nucleus, which act as a medium for direct communication between different cortices forming a transthalamic pathway (Sherman and Guillery, 1996; Rouiller and Welker, 2000; Mo and Sherman, 2019). Additionally, some inputs act as *drivers* while others act as *modulators* (Sherman and Guillery, 1998, 2011). Driver inputs provide the primary excitatory signal of information while modulators affect how driver inputs are relayed in terms of their confidence (or precision) level (Kanai et al., 2015). They are distinct in many ways. For instance, their gating function is based on distinct synaptic features where drivers typically show paired-pulse depression<sup>4</sup> with large excitatory postsynaptic potential (EPSP), whereas modulators show paired-pulse facilitation with small EPSPs.

In favor of the predictive brain hypothesis (Friston, 2005; Frith, 2009), HO feedback (backward) connections from the cortex to the thalamus outnumber the FO feedforward connections by 5–10 fold (Guillery, 1995; Sherman and Guillery, 2006), suggesting that sensory processing rely less on FO driver inputs and more on HO feedback inputs from the cortex (Wolff et al., 2020). We view the prevalence of backward connections as the predictive (active) attitude of the brain in a similar way as argued in 4E cognition. Thus, the pulvinar, being the HO nuclei in the visual system, is actively contributing to the cortico-cortical pathways by way of transthalamic connections, i.e. cortico-thalamo-cortical connections, qualifying as a candidate for the behavior-related information (Benevento and Port, 1995).

### 2.4. Transthalamic transmission

Under the predictive brain hypothesis, ascending prediction errors provide newsworthy information through numerous sensory channels unpredicted by the descending signals. Ascending signals compete to update the descending predictions with different encoded levels of confidence. This updating mechanism is reflected in the excitability of neuronal populations so that through neuronal gain, sensory channels of high confidence pass through the filter and influence descending predictions of multiple cortical regions. This places the pulvinar in an important position as the descending inputs to the pulvinar derive from cortical feedback pathways that enable the LGN and pulvinar to regulate the transmission across the visual cortex relative to behavioral and cognitive requirements (Saalmann and Kastner, 2009). As behavior depends on the integration and interaction between multiple cortical areas as well as the body and environment we take transcortical transmission to be of principal importance (Cisek and Kalaska, 2010; Sherman and Usrey, 2021). This consequently renders the thalamocortical architecture a qualified candidate in explaining the functional relations between EFs and SMRs. Several studies have demonstrated the importance of the thalamus in cognitive processes with a gradually converging view on the function of the thalamus (Mitchell and Chakraborty, 2013; Mitchell et al., 2014; Mitchell, 2015; Mukherjee et al., 2020, 2021).

Saalmann and colleagues (2012), for instance, showed that the pulvinar synchronized the activity between cortical areas (visual and temporal cortex), providing evidence that the pulvinar has a critical role in regulating information transmission across the visual cortex. They did so by simultaneously recording pulvinar spike and local field potentials from area V4 and the temporo-occipital area (TEO) of monkeys. They showed that when directing attention to the receptive field of neurons in V4 and TEO, spike-field coherence between the pulvinar and the alpha-band oscillations in these areas was significantly enhanced. Specifically,

<sup>4</sup> Paired-pulse depression refers to the postsynaptic decrease when given paired-pulse stimulation, i.e. impulses closely following one another. Paired-pulse facilitation refers to the increase in evoked postsynaptic potentials.

<sup>3</sup> We refer to neocortex as cortex throughout the paper.

conditional Granger causality analysis revealed that the LGN was driving the alpha rhythms while the pulvinar predominantly modulated the alpha frequency. These results imply that the pulvinar is facilitating the intercortical transmission of visual information by synchronizing cortical alpha activity. Several studies have since shown that the modulation capacity of the pulvinar includes attentional control and cortical synaptic gain (Purushothaman et al., 2012; Zhou, Schafer and Desimone, 2016; for review: Halassa and Kastner, 2017). But how do descending predictions regulate behavior and information transmission relative to environmental change?

### 2.5. Environmental change and self-motion

With regards to prediction-driven inputs to the pulvinar, several studies show strong evidence that the neuronal characteristics of descending signals in layer 5 of V1 and V2 to the pulvinar are of a driver-kind (Sherman and Guillery, 2002, 2006; Guillery, 2005; Mease and Gonzalez, 2021) bursting roughly every 100 ms, i.e. alpha frequency (Silva, Amitai and Connors, 1991; Flint and Connors, 1996; Buffalo et al., 2011; Spaak et al., 2012; Foster et al., 2017), whereas projections from layer 6 to the pulvinar are considered to be modulatory (Moore et al., 2019; Abbas Farishta, Boire and Casanova, 2020). It is also known that the pulvinar conveys diverse contextual information to the visual cortex about the sensed environment that was not predicted by self-motion (Roth et al., 2016). Similarly, responses in V1 can be modulated by the animal's locomotion (Niell and Stryker, 2010; Keller, Bonhoeffer and Hübener, 2012; Saleem et al., 2013). Descending projections relevant to environmental change and self-motion materialize through the integrative role of the pulvinar.

This is supported by a recent study by Blot and colleagues (2021) who sought to better understand environmental change versus self-motion in the pulvinar of mice using virtual environments. After training mice to run through virtual corridors consisting of gratings on the walls that change according to their self-motion on a running wheel, Blot et al. (2021) decoupled the visual information, i.e. optic flow, from the self-motion of the trained mice by playing the virtual corridor at different speeds. The gratings on the walls would then, for instance, be played at a faster pace compared to the running wheel and thus the self-motion of the animals. The aim was to uncover how, at a neuronal level, the mice accounted for the incongruence between the rate of change in environmental sensation relative to their self-motion. They found that the pulvinar not only transmitted optical flow signals but also environmental information relative to the mice's locomotion. Intracortical transmissions showed that V1 conveyed mainly visual information about the rate of optic flow to the anterolateral area<sup>5</sup> (AL; higher visual structure), while projections from the pulvinar to AL revealed integrated signals with both information related to the environment and self-motion (Fig. 2). Strong descending (driver) inputs from layer 5 of V1 and descending (modulatory) inputs from layer 6 of higher cortical structures to the pulvinar suggested how the transmission from the pulvinar up to layer 4 in higher visual structures appear to reflect the integrated confidence between the expected optical flow during self-motion, i.e. "how fast the environment changes when I move this fast", and the environmental optical flow speed. Interestingly, the projections from layer 5 also function as the cortical input to the basal

<sup>5</sup> The anterolateral area is an area specific to the mouse brain. It is part of the visual area and is further related to the processing of movement in the environment while providing self-motion cues to the area relevant to spatial cognition.

ganglia which is responsible for action-related processes (Shipp, 2005, 2007). These results display the functionality of the HO nuclei as both integrative and informative (Aton, 2021). In summary,<sup>6</sup> transthalamic pathways integrate signals from V1 with information from higher visual areas, e.g. V4 and middle temporal area (MT) that is involved with visual motion (Fig. 2B).

### 2.6. Pulvinar encoding confidence

According to predictive coding, the sensorimotor incongruence can be resolved by attenuating the precision of sensory signals involved with self-motion. Such attenuation of precision, as suggested above, sits well with the pulvinar as it integrates the environmental changes and self-motion. Descending predictions become updated based on prediction errors guiding the adaptive coordination of visually guided behaviors by regulating the confidence levels reflected in the pulvinar (Saalmann and Kastner, 2009; Saalmann et al., 2012; Komura et al., 2013; Kanai et al., 2015). Thus, for EFs to modulate behavior, sensory channels must be of high precision biasing transthalamic projections in a predictive coding manner, which results in modulation of behavior. As mentioned above, descending projections from layers 5 and 6 in the cortex to the pulvinar convey prediction errors that allow the pulvinar to estimate the precision (Kanai et al., 2015). Environmental modulation can thus occur when SMRs convey mismatching information with high precision, biasing the behavioral outcome. In what follows, we describe how SMRs relate to EFs and how that relation can be quantified. Finally, we review studies that have modulated EFs to automatically influence behavior.

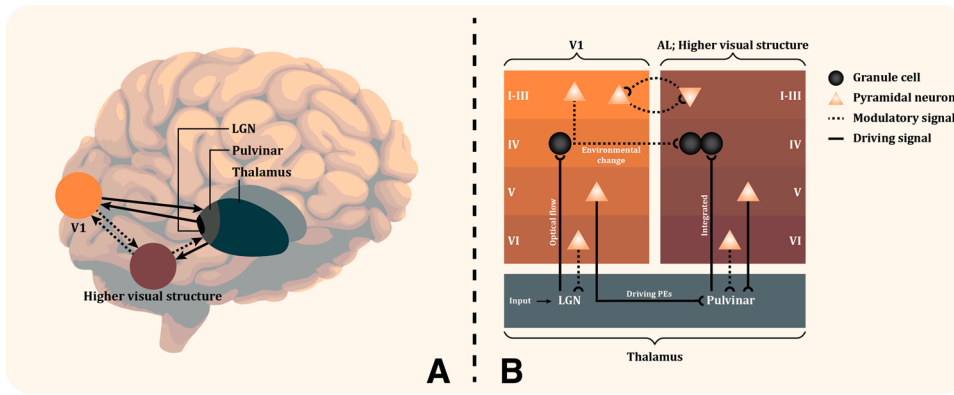
## 3. Environmental features

### 3.1. Affordances

In his book, James J. Gibson (1986) coined the term *affordances*, which refers to the behavioral possibilities an environmental setting offers a specific human agent. The way we portray affordances relates to Di Paolo, Buhrmann, and Barandiaran (2017) in the sense that sensorimotor schemes compose a broad network of affordances that directly involve (i) the agent's sensorimotor covariations, (ii) the reliable action trajectories, (iii) the goal-oriented coordination, and (iv) the task or situation of the agent (2017, p. 81). The schemes refer to the frequently applied and efficient organization of sensorimotor patterns for achieving a specific goal in a specific situation, which also paves the way for how associations arise (Fig. 3). Each scheme then reflects an affordance, i.e. an interactive cycle between the sensed environment and adaptive motor processes, just as turning a sharp corner resonates with slowing down.

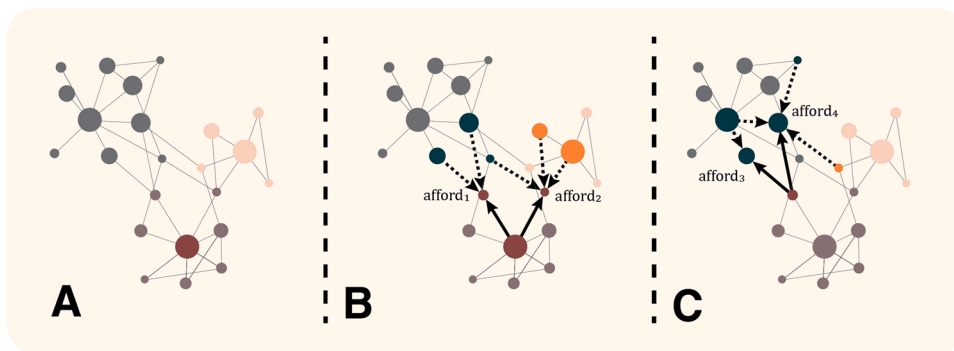
The structure of sensorimotor schemes depends on the environmental solicitations but is not determined by them alone. Instead, as any situation is met by a repertoire of history-dependent sensorimotor schemes, the selection and modulation of the schemes comprise an attunement process that effectively influences the competition between afforded schemes. The history dimension introduces the possibility to associate prior experience by affecting the dynamic decision-making process backward, i.e. top-down. This is because SMRs can be associated with the agent's existing repertoire of sensorimotor interactions, generating expectations about motor processes and sensory impressions. SMRs contribute to the organization of affordances by conceptually foreshadowing them, e.g. one predicts the act of *pushing* but only after *turning the doorknob*. Affordances can thus be considered as the range of

<sup>6</sup> It is worth noting that several studies referred to above are based on either rodent or monkey brains, however, there is evidence that transthalamic pathways bridging cortical areas also applies to the human brain, suggesting that this may be a feature of the mammalian brain (Villeneuve et al., 2005, 2012; Mo and Sherman, 2019).



**Fig. 2.** Minimal model of transthalamic projections. A. A conceptual diagram illustrating the projections from LGN, i.e. FO nucleus, to the primary visual area, which then projects back to the pulvinar, i.e. HO nucleus, before projecting back up to higher visual structures, e.g. V4, middle temporal area, or inferior temporal cortex. The pulvinar thus takes the role of a mediator between cortical areas providing it a possibility to transform and integrate information. Our framework suggests that it integrates confidence levels about sensory processes that further affect the higher visual cortex together with the corticocortical projections. The color of the arrows reflects from where the projection originates. Dashed lines reflect modulatory signals while solid lines illustrate driving signals. B. This illustrates the neurophysiological scheme underlying the transthalamic pathway

and demonstrates how the pulvinar acts as an integrative hub. This view shows the thalamus as being actively engaged in the continuous processing of information between cortical areas rendering the transthalamic architecture to be of particular interest. The triangles illustrate pyramidal neurons while the black circles illustrate granule cells. Dashed lines illustrate modulatory signals while solid lines illustrate the driving signals. The anterolateral area (AL) of the mice corresponds to higher visual structures in the human brain. We have omitted projections that have not been mentioned.



**Fig. 3.** Three stages of a fictitious sensorimotor scheme network. A. This is a given agent's network of sensorimotor schemes, involved with some ongoing task (big red sphere). Each node corresponds to a sensorimotor scheme that consists of an interactive cycle between agent and environment, e.g. walking on steep terrain needs an adaptive gait. This figure also illustrates the structural network with all possible relations between schemes. All lines between nodes are similar. B. Upon engaging with soliciting features of the environment, the agent makes use of prior experienced sensorimotor dynamics causing certain schemes to compete for engagement. Here, *afford<sub>1</sub>* and *afford<sub>2</sub>* are competing for engagement, illustrated in the diagram as blue spheres receiving

directed bold arrows. The dashed arrows illustrate associated affordances also affecting the competition for engagement top down. Internal demands can elicit these dynamics as well. C. Essentially, the dominating scheme enacts a specific kind of behavior and dynamically causes new interactions with the environment, which then continues the affordance competition for engagement. Here, *afford<sub>3</sub>* and *afford<sub>4</sub>* immediately engage in competition. The illustration is drawn with inspiration from Di Paolo, Buhrmann, and Barandiaran (2017).

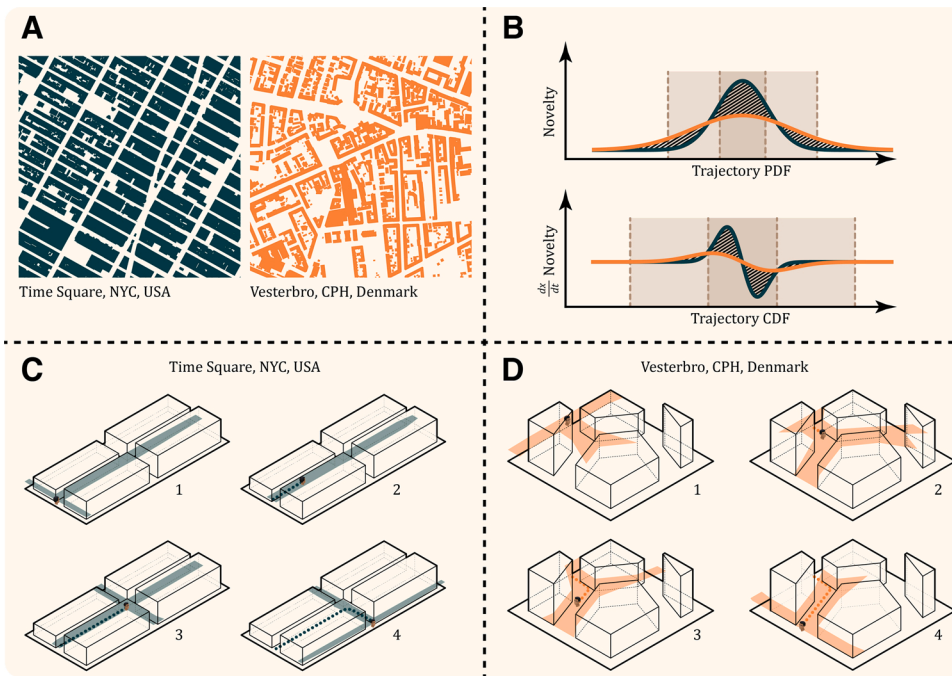
prospective actions depending on the action-related properties of the environment and relevant norms. It is, in other words, a future-oriented concept asking *how can I act given this body, history, habits, and situation*. This enactive approach is thus also, at heart, a different project than the ecological psychology approach to free energy principle (but see, Flament-Fultot, Nie and Carello, 2016; Heft, 2020; Read and Szokolszky, 2020).

In the biogenic sense, affordances reflect the essence of *allostasis*, which is the anticipatory process that proactively predicts the outcome of a situation before it can have a potentially lethal impact on the homeostatic process (Corcoran, Pezzulo and Hohwy, 2020). By predicting the environment and the appropriate actions, we adapt and improve our chances of remaining alive, which is the objective of a living organism. This is essentially the critical argument for the hypothesis of the predictive brain (Friston, 2010). The internal environment of a living organism is changed by way of homeostatic regulations, while the perception of the external environment is changed by way of moving around using sensorimotor schemes. The interdependency of action with allostasis highlights that humans are undeniably entangled with the possibilities for action. To handle these possibilities, we rely on several processes on the fly, from immediate sensations to past experiences, to make informed behavioral decisions in a winner-takes-all fashion

(Pezzulo and Cisek, 2016). Additionally, by automatically relying on SMRs, we are allocating resources to other more sophisticated tasks that need our awareness.

### 3.2. Identifying environmental features

What are environmental features (EFs)? EFs are distinct aspects of the built or natural environment that resonates with an SMR—however, we distinguish between *EFs* and *SMRs* as the former relates to the design of the built environment, whereas the latter refers to the sensorimotor responses of an agent. They are functionally coupled through the dynamics of the brain, body, and environment. The interaction with EFs carries features that are functionally associated with specific possible actions. One such feature, which we will focus on, is the rate of change of sensory information in the visual system during motion. To reiterate, the optical flow, which reflects the direction and rate of sensory change given some action, reveals the direction and distance between an object and an organism by accounting for self-motion (Gibson, 1966, 1986). In what follows, we particularly investigate the act of turning a blunt corner as it affords slow changes in the rate of sensory change as opposed to sharp corners (Fig. 4). We then extend our analyses to demonstrate that these EFs harmonize with distinct SMRs and then we finally review



**Fig. 4.** An overview of how urban structures affect SMRs and an example of how an isovist simulation unfolds. A. Noll maps of a central portion of Copenhagen, Denmark, and a central portion of New York City, USA. The sudden rapid growth of Copenhagen is reflected in the organic and loose urban planning of the city. In contrast, New York City and other major cities in America underwent the orthogonal and strict division of areas. A stroll in Copenhagen is arguably different from a stroll in New York City in terms of the frequency of sensory information. B. This graph depicts the amount of novel sensory information collected in New York City (blue) and Copenhagen (yellow). For New York City, the novelty is initially flat until the turning of a corner elicits a short, high burst of new sensory information before becoming flat again. Copenhagen displays a slow but constantly increasing amount of information with much longer corners in terms of collecting sensory information. The urban structures offer distinct EFs. The (brown) dashed areas in the background display where the features differ. The lower graph displays the derivative. C. This series of illustrations demonstrate a single subset of New York City to exemplify Space Syntax analysis in acquiring new sensory information. The blue area depicts the area of visible space from a given point in the urban space (isovist). Note the *homogeneity* of the area as the stroll

unfolds. D. Examining a single subset of Copenhagen using Space Syntax analysis. Note the *heterogeneity* of the area as the stroll unfolds.

studies that used EFs to alter behavior according to the rate of change so that one either speeds up or slows down our action.

Designing spaces with a high rate of visual flow will make it appear as if one is speeding up because the high rate of environmental sensory information is associated with moving at higher speeds. This may either solicit the act of speeding up or slowing down, depending on the current state and prior experiences of the person in question. One can think of SMRs as arguments (conditioned on confidence and based on associations and prior experiences) for how the trajectory of actions should unfold throughout our network of associated actions. They initiate and relate soliciting actions conditioned by our predicted confidence about that specific feature. This can result in a bias of behavior and cognition as certain features carry relatively high confidence. As a proof of concept, we analyze two kinds of EFs to demonstrate that different environments cause different sensory responses reflected also in motor behavior.

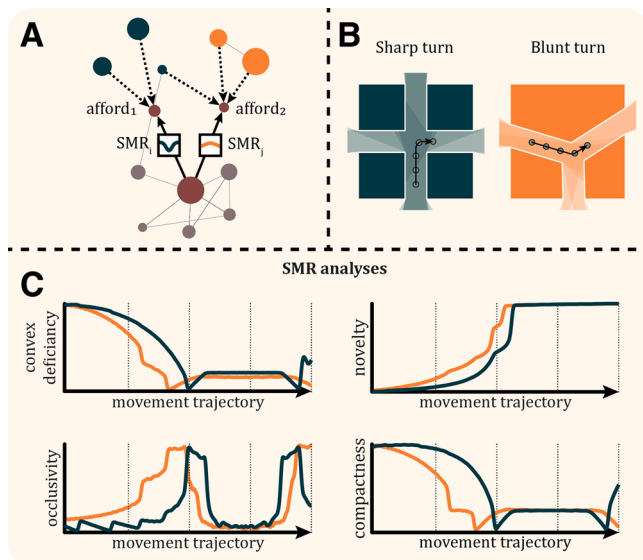
Several dynamics between agent and environment have been quantified using Isovist and Space Syntax, i.e. mathematical quantification of spatial configurations (Benedikt, 1979; Hillier and Hanson, 1989). Isovist quantifies the relation by representing the agent, in two-dimensional space, as a single point that projects radial vectors from its center towards the environment, where the environment functions as obstructions that in turn provides a planar geometrical shape of the space between agent and environment (Fig. 4B). By drawing a walking-path through the environment, several parameters describing the dynamics between agent and environment can be extracted. These have also been correlated with traits of human behavior (Stamps, 2005; Wiener et al., 2007). Beware, extracting information from two-dimensional features is a simplified approach compared to richer three-dimensional features. Based on the simplified approach, we analyzed four dynamics to demonstrate that subtle changes in the environment can lead to distinct SMRs and thus contribute to cognition and behavior in distinct manners (Fig. 5):

1. *Oclusivity* was described first by Gibson (1966) and later quantified by Benedikt (Benedikt, 1979) as the length of the occluding radial boundary of the isovist shape.
2. *Compactness* corresponds to the ratio of the perimeter squared and the circularity of the area;  $\frac{perimeter^2}{4\pi \cdot area}$ , that is, the circumference of the isovist shape relative to a circle.
3. *Convex deficiency* corresponds to the difference between the area of the convex hull of the isovist shape and the area of the isovist shape divided by the area of the isovist shape;  $\frac{convex\ hull\ area - isovist\ shape\ area}{isovist\ shape\ area}$  (Stamps, 2005).
4. *Novelty* treats each collision point with the environment as unique and corresponds to the cardinality of the collected set of collision points, adding only those that has not yet been encountered by the agent;  $\sum_t |collision_t|$

### 3.3. Error dynamics

Under predictive coding, SMRs effectively amount to the error dynamics in sensory channels, which have also been linked with both the appreciation of visual art (Van de Cruys, 2017) and well-being (Miller, Rietveld and Kiverstein, 2021), during some action. The error dynamics depict the predictability of sensory information based upon actions and prior experiences given the current circumstances. With high confidence in sensory predictions, action can be modulated by the error dynamics in the sensory channels. To provide an example, the calm atmosphere that one might find in certain natural areas can automatically give rise to deceleration of actions that are associated with that environment while, similarly, urban city centers with their rich sensory information can automatically give rise to accelerated actions, which is also associated with that environment. While the embodied brain is automatically attentive to EFs, we are free to be aware of other things that are cognitively more demanding, e.g. planning our day, going over the shopping list, internal monologue, etc., all while the embodied brain adapts to the sensed error-dynamics.





**Fig. 5.** A conceptual example of how different EFs are related to different SMRs. A. In this example, we consider how two distinct EFs can lead to distinct behaviors that resonate with the perceived dynamics. One may favor *afford<sub>1</sub>* because the specific SMRs are associated with specific reliable action trajectories under those circumstances. In a phrase; given a specific *SMR<sub>i</sub>*, the agent has reliably favored *afford<sub>1</sub>* according to the agent's norms. The two solid arrows point through two distinct dynamics, i.e. *SMR<sub>1</sub>* and *SMR<sub>2</sub>*, that are both associated with distinct behaviors, i.e. *afford<sub>1</sub>* and *afford<sub>2</sub>*, that the agent has relied upon previously. B. By applying Isovist, the sensed environmental changes for an agent traversing from one space into another, differing in their angle of turn, generates distinct sensory dynamics known to alter behavior (Stamps, 2005; Wiener et al., 2007). The yellow space (left) has a blunt transition as compared to the blue space (right). The gray dots in the center corresponds to the agent's position where the viewing direction is illustrated by the solid color. C. Notably, by simply altering the angle of turn, the parameter analyses of occlusivity, convex deficiency, compactness, and novelty display strong differences. These serve as examples of how distinct EFs relative to a moving agent can be associated with distinct SMRs.

#### 4. Psychobiological evidence

In 1903, Georg Simmel, a German sociologist, wrote an essay, *The Metropolis and Mental Life*, evaluating the psychological impact the city affords compared to the rural districts. The evaluation builds on the increased nervous stimulation that results from the high tempo, constant sensory exposure, and changing impressions of the city as opposed to the lasting impressions with slight changes in rural districts. Here, sensory impressions flow more slowly and more evenly. In his own words: "The psychological foundation, upon which the metropolitan individuality is erected, is the intensification of emotional life due to the swift and continuous shift of external and internal stimuli [...] To the extent that the metropolis creates these psychological conditions – with evert crossing of the street, with the tempo and multiplicity of economic, occupational and social life – it creates in the sensory foundations of mental life, and in the degree of awareness necessitated by our organization as creatures dependent in differences [...] Thus the metropolitan type [...] creates a protective organ for itself against the profound disruption with which the fluctuations and discontinuities of the external milieu threaten it." (Simmel, 1995, pp. 31–32). Although Simmel takes the argument much further, the notion that the rate of change in sensory impressions, e.g. optical flow in visual sensation, is an important feature for cognition and behavior is conspicuous. One such feature, as we have argued, is the structure of spatial transitions in the turning of a corner that vary depending on primarily the angle. Cities have made use of various solutions (Fig. 6). This is not to say that cities are detrimental, but rather that the built environment exploits adaptive capacities through meaningful and beneficial

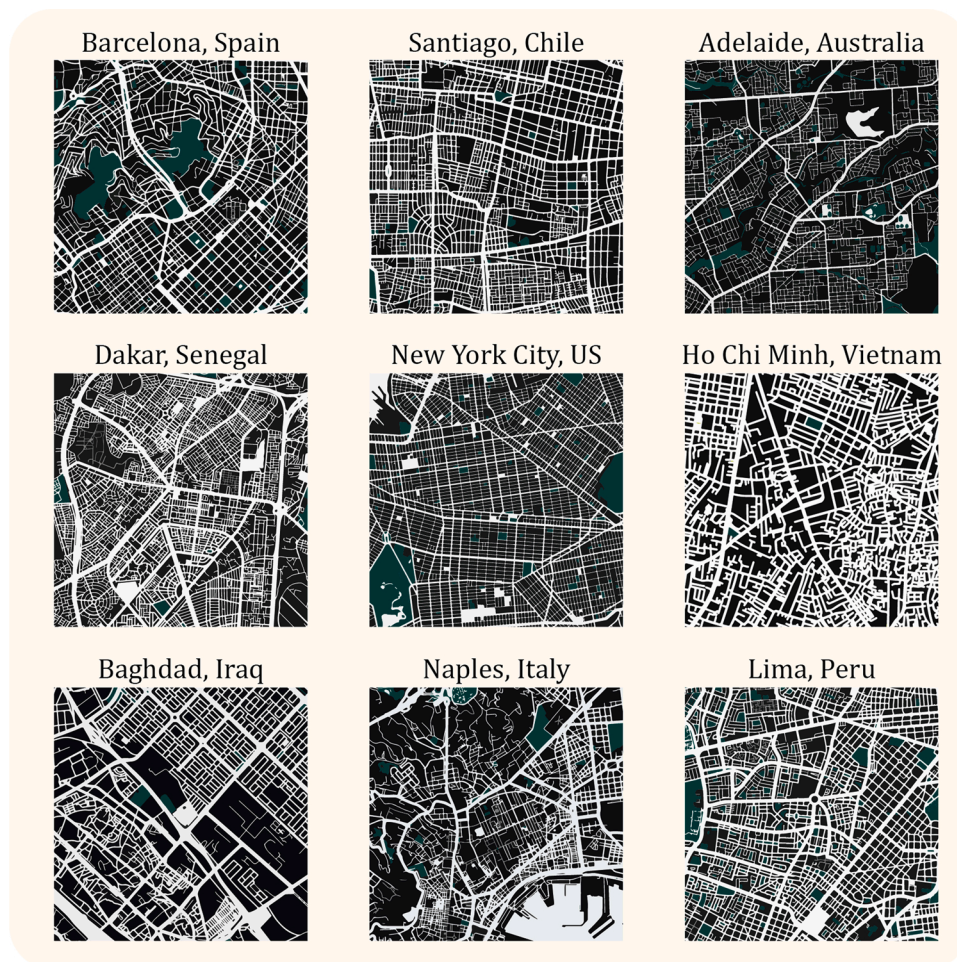
manipulations.

An example of advantageous manipulation of optical flow in everyday life to adjust behavior is *Chicago's Lake Shore Drive* cited in Thaler and Sunstein (Thaler and Sunstein, 2021, pp. 46–48). As the drive stretches along the east coast of Lake Michigan, it offers a series of S-curved turns and a stunning view of Chicago's architectural skyline causing drivers to fail to slow down resulting in numerous unfortunate wipeouts. Instead of introducing speedbumps or the like to encourage speeding down, the city chose to decrease the distance between the white stripes painted onto the road when approaching the dangerous curves so that the sensory dynamics associated with high velocity is implicitly affecting our attunement causing a change in the scheme network and eventually expressed behaviorally in slowing down. This rather simple intervention requires no awareness of the white stripes themselves as the reviewed studies above suggest. It instead suggests that the bias occurs rather early in the process (Rakha, Katz and Duke, 2006). The white stripes correspond to the EF while the act of slowing down based on associated sensory dynamics is the SMR.

A similar conclusion was reached by Manser and Hancock (2007) when they studied the driving speeds in cars passing through tunnels. Using a Driving Environment Simulator, participants were asked to maintain a fixed speed limit throughout their drive through a tunnel. Once the participants reached the predetermined speed, the speedometer was removed from their view, demanding the participants to use their visual perception of the tunnel to adjust their speed. By changing the frequency of vertical lines on the tunnel walls, the researchers discovered that speed limits could be altered. If the vertical lines were wide, which is typically associated with moving with low velocity as it provides a slower rate of change, the participants speeded up significantly as compared to thin vertical lines, which is typically associated with moving with high velocity as it provides a high rate of change. The study concludes that the speeds adopted by the drivers could be influenced significantly by the application of visual patterns to a typical transportation environment.

Affordances and sensorimotor brain dynamics have recently been demonstrated to be linked in two studies by Djebbara and colleagues (2019; 2021). The authors asked human participants to transit from one virtual space to another through a door, whose width varied between trials, to answer how EFs that appeal to specific actions informed perceptual processes. The width of the doors varied between trials so that one of three possible doors was impassable. This altered the affordances of the transition. Applying a combination of Virtual Reality and MoBI to assess the brain dynamics upon perceiving the door, the authors demonstrated both the movement-velocity in approaching the door and the early perceptual processes over the sensorimotor cortex reflected the affordances of the door. The two doors that were of different sizes but both passable were indissociable in terms of movement-velocity and cortical responses, whereas the impassable door was significantly different. Furthermore, they also demonstrated that the same affordance pattern emerges on the frequency level of neuronal oscillations. Alpha desynchronization over the parietal and visual cortex reflected the affordances of the door. In other words, EFs have evoked SMRs in the embodied brain related to early perceptual processes, reflected in the participants' behavior.

The behavioral results found by Leonards et al. (2015) support this contention. In questioning whether the tile-pattern direction on the floor can modulate walking direction, Leonards and colleagues (2015) had human participants perform a rapid serial visual presentation task while walking straight ahead on varying tile-pattern directions. Their study found that participants veered significantly away from the straight trajectory in their baseline when walking over patterns that were close to the straight line, but not if the pattern direction was rotated too far off the straight line. Interestingly, none of the participants reported noticing the floor pattern to have changed between trials suggesting a behavioral impact of covert attention without awareness. The behavioral effect was only measured when the pattern direction did not differ too much from



**Fig. 6.** Nine examples of Nolli maps around the world, where the use of rectangular grids for city planning collide with amorphous and naturally grown parts of the same city. The two distinct ways of planning cities also have two distinct features of sensorimotor dynamics, which include different ways of affecting neuronal processes by, for instance, the turning of the head (head direction cells), body posture (body schema), and the rate of change in sensory information (thalamic nuclei). As the brain makes use of global patterns in cognitive processes (Lachaux et al., 1999; Varela et al., 2001), cities have an impact on cognition for better or worse.

the straight, which is when uncertainty in the predicted sensory signal is the highest. With a higher top-down uncertainty follows a greater bottom-up bias. The closer the pattern directions become the more difficult they are to dissociate and we thus rely on bottom-up signals. We interpret these results as; the sensory responses of the patterned tiles (EFs) have implicitly affected the attunement to the environment expressed in behavior (for a review on the behavioral impact of visual patterns, see: Wilkins, Penacchio and Leonards, 2018).

Another take on the importance of the flow of sensory information is demonstrated by Ludwig et al. (2018), who shows that altering the optical flow affects the walking speed in human locomotion. Ludwig and colleagues asked their participants to walk down a walkway on which they had projected stripes oriented orthogonal to walking direction with varying distances. While walking down the walkway, participants were asked to perform a perceptual discrimination task involving the orientation of a bar projected to the back wall. In line with our account, they consistently found a decrease in walking speed when the distance between the projected lines decreased, i.e. higher frequency of lines in optical flow. They found the same pattern of effect when increasing the distance between projected lines, i.e. an increase in walking speed. Our suggested framework proposes that the sensed rate of change of lines on the ground taints the automatic behavioral decision on walking speed because a high velocity of optical flow has reliably been interpreted as “I am moving fast” in the past. The modulation of optical flow on locomotion has been demonstrated several times (Pickhinke, Chien and Mukherjee, 2014; for instance; Pechtl, Jennings and Redfern, 2020).

It is not surprising that animals make use of the same strategy in guiding their behavior. In the excellent study by Bhagavatula and colleagues (2011), they had budgerigars fly through a tunnel with either

horizontal or vertical lines on either the left or right wall. In combining the line directions with the walls, they demonstrated that the change in line direction not only caused a significant change in flight velocity of budgerigars but also a change in their trajectory so that they fly closer to the vertical lines. However, the horizontal lines made the budgerigars fly significantly faster. Interestingly, as the horizontal and vertical lines enact distinct responses, they also altered the afforded behavioral outcomes in distinct ways. This strategic use of visual control has also been observed with hummingbirds (Dakin, Fellows and Althuler, 2016), honeybees (Srinivasan et al., 1996; Baird et al., 2005), and bumblebees (Dyhr and Higgins, 2010). It may be a general strategy, adopted from early developments of the brain, to associate specific EFs with specific SMRs.

These studies make it clear that the processing of sensory information, i.e. rate of change in sensory information, has an impact on cognition and behavior as it can be translated into a question of how self-motion and the visual environment get integrated. But is it possible to develop experiments that can assess the impact? As intracranial studies of transthalamic transmission are remarkably rare in human beings, neuronal markers of such transmissions are highly valuable. Accumulating evidence suggests that slow cortical alpha rhythm over occipital areas reflect exactly such transmission (e.g., Steriade et al., 1990; Llinás et al., 2005; Fries, 2015; Halgren et al., 2019; Seeber et al., 2019), we thus briefly suggest here another equally important parameter, namely the possibility of recording brain activity of freely moving human beings.

## 5. Future studies using Mobile Brain/Body Imaging

Analyzing the transthalamic pathway requires a combination of sophisticated neural modeling techniques and mobile neuroimaging techniques that allow human beings to freely act in their surroundings. We thus turn here to the question of how future studies can contribute to the study of SMRs and EFs. Traditional experimental protocols eliminate potentially confounding factors with movement being considered such a confound. The advantage of traditional and highly controlled experimental protocols in isolated experimental setups is that they allow for precise analyses of the factors of interest while eliminating potential confounding factors. For instance, looking at two-dimensional images of three-dimensional spaces allows for investigating brain activity accompanying visual intake of defined information provided with each image. At the same time, confounding factors, e.g. other visitors, sounds and smells, or movement-related artifacts in the recording can be controlled. As such, the visual experience and their constitutive brain dynamics can be investigated in isolation. But it seems questionable whether the results from such experiments resemble the embodied human experience when exploring museums, schools, or cities. The continuous changes in predictions and affordances—be it visual, proprioceptive, acoustic, etc.—while moving through the built environment will, by definition, lead to changes in brain dynamics reflecting the neural processing of all bottom-up and top-down information streams. The brain dynamics resulting from active movement through urban exploration will differ drastically from the ones accompanying visual processing of images of the city, rendering the ecological validity of traditional experiments rather low. Thus, investigating human brain dynamics accompanying the holistic experience of the built environment requires new neuroscientific methods and data analysis protocols.

MoBI is such a method that developed rapidly over the last decade and today provides new insights into human brain dynamics during interactions with real and virtual environments. Recent technological developments have overcome the restrictions on mobility by developing mobile and lightweight amplifiers that allow for investigating brain dynamics even in moving participants. Particularly the combination of mobile brain activity recordings, motion capture, and data-driven analysis approaches has provided promising results in this regard (Makeig et al., 2009; Gramann et al., 2011, 2014). From virtual scenarios with controlled but highly immersive applications merging high-density EEG with motion capture and other measures (Banaei et al., 2017; Djebbara et al., 2019; Gehrke and Gramann, 2021) to natural interactions with the built environments using low density portable EEG systems (Wunderlich and Gramann, 2021) or even unobtrusive low-density ear EEG (Hölle, Meekes and Bleichner, 2021). Pipelines for the standardized analyses of multi-modal data (Klug and Gramann, 2021; Klug et al., in prep) or automated online correction during the recording of the data (Mullen et al., 2015) are available open-source and are continuously extended for the scientific community. The future of MoBI lies in continuous unobtrusive recordings of human brain activity using EEG or mobile MEG (Optically Pumped Magnetometers; Seymour et al., 2021, 2022) together with context information about EFs, e.g. eye-tracking, scene cameras, continuous GPS-based position, and Augmented or Virtual Reality in systematically-studied conditions (Parada, 2018). Furthermore, among other features such as consciousness and self-awareness, intrinsic neural timescales are a key mediator in behavioral and cognitive processes (Northoff, Wainio-Theberge and Evers, 2019). With the relevant neuronal architecture identified, future laboratory research could also focus on the systematic temporal relationship between intrinsic neural timescales (INTs) and EF-SMR mechanisms (Northoff and Huang, 2017; Northoff, 2018). There is, for instance, the relationship between fast INTs of unimodal regions, e.g. visual cortex, and the slow INTs in transmodal regions, e.g. default mode network, which may provide crucial insights to the difference between slower but higher-order semantic interpretation of the environment versus fast but lower-order sensory dynamics. The temporo-spatial

theory of consciousness (TTC) may prove to be a more fruitful approach (Golesorkhi, Gomez-Pilar, Tumati et al., 2021; Golesorkhi, Gomez-Pilar, Zilio et al., 2021; Wolff et al., 2022).

Returning to the above-described gating mechanisms and transthalamic transmission, decades of recordings of electrical brain activity in humans using electroencephalography (EEG) have demonstrated pronounced modulations of the alpha frequency band in sensory areas (Klimesch, 1997, 2012; Llinás et al., 1998; Foxe and Snyder, 2011). This frequency band centered around 10 Hz reflects cortico-thalamo-cortical coupling, rendering MoBI a prime methodological window into the ecological brain dynamics of human experiences. The early neurophysiological entanglement between self-motion and visual context is not directly measurable using MoBI as it unfolds at a subcortical level. However, as the process is at least partly reflected in the alpha band oscillation that is measurable using high-density MoBI (Do, Lin and Gramann, 2021; Gramann et al., 2021), these deeper structures can successfully be approached using biophysically plausible causal modeling to infer their contribution to the measured activity (David et al., 2006; Garrido et al., 2008; Seeber et al., 2019). It requires a generative model that combines superficial and deep neural models of the brain hypothesized to explain the activity. This has successfully been done by generic dynamic causal modeling (Boly et al., 2011; van Wijk et al., 2018). The advantage of generative models is that the simulations possible with such methods can help elucidate how unbuilt spaces could affect their future users, e.g. schools, kindergartens, offices, urban spaces. Importantly, such models will consider both physiological and behavioral dynamics while comparing and mapping people's subjectively constituted environments. Combining measurements of the alpha band oscillation with causal modeling yields a robust approach that allows for maximizing ecological validity and thus for new insights into the relation between EFs and SMRs.

## 6. Concluding remarks

We aimed to synthesize the behavioral with the neurophysiological views of how EFs affect behavior and cognition through SMRs. To do so, we introduced a psychobiological framework that builds on the enacted and predictive brain. We defined SMRs through transthalamic transmissions and EFs as features that resonate with specific SMRs. Introducing the sensorimotor network of schemes demonstrated how EFs and SMRs are related. This advanced our understanding of how visual control biases behavior by mapping the associated sensorimotor relations between afforded actions. The trajectory through the network could be explained through SMRs and our confidence in these, which become the reason why one action would be chosen over another.

We applied the framework to the reviewed behavioral and neurophysiological studies of how human beings and other primates automatically rely on their context in the forming of behavior. As neurophysiological studies of *in vivo* and *in actio* human beings are technically difficult, we have relied here on studies on mice and monkeys to identify how such biases can occur. These studies elucidated that the transthalamic pathway is of high importance as the integration between self-motion and contextual change depends on this mediator between cortical areas. Although we have mainly targeted the capacity of attention, we see how other human capacities and behaviors can be altered based solely on environmental interventions. We finally suggested how future studies can use the combination of MoBI and sophisticated modeling techniques of the brain to answer questions about how EFs and SMRs are interrelated.

Although we conclude that EFs can have an automatic impact on cognition and behavior, our psychobiological framework has only taken the first steps in understanding the underlying neuronal process that accounts for the bias. It was furthermore limited to the human attentional capacity. It remains unknown whether memory, decision-making, and other capacities are affected similarly. There may also be a multitude of features that can be extracted from the ongoing attunement

using Isovists and Space Syntax and further be related to the activity of the brain (Javadi et al., 2017). The integrative transthalamic pathway has proven to be of high importance in this particular case, however, it remains unknown whether it also accounts for other biases. In this sense, the research of how the design of cities and buildings affects the human brain and body cannot be considered a matter of *nice-to-have*, but rather *need-to-have*. The design of the environment is not a matter of empty splendor, but a responsibility of creating reasonable settings in society for the future. More empirical and modeling studies are needed to better understand how the omnipresent built environment is continuously affecting the human brain.

## References

- Abbas Farishta, R., Boire, D., Casanova, C., 2020. Hierarchical organization of corticothalamic projections to the pulvinar. *Cereb. Cortex Commun.* 1 (1), tgaa030.
- Adams, R., et al., 2013. The computational anatomy of psychosis. *Front. Psychiatr.* 47. Available at: <https://www.frontiersin.org/article/10.3389/fpsy.2013.00047>.
- Adams, R.A., Shipp, S., Friston, K.J., 2013. Predictions not commands: active inference in the motor system. *Brain Struct. Funct.* 218 (3), 611–643. <https://doi.org/10.1007/s00429-012-0475-5>.
- Anton-Erxleben, K., Carrasco, M., 2013. Attentional enhancement of spatial resolution: linking behavioural and neurophysiological evidence. *Nat. Rev. Neurosci.* 14 (3), 188–200. <https://doi.org/10.1038/nrn3443>.
- Aton, S.J., 2021. Aligning one's sights: the pulvinar provides context for visual information processing. *Neuron* 109 (12), 1909–1911. <https://doi.org/10.1016/j.neuron.2021.05.028>.
- Baird, E., et al., 2005. Visual control of flight speed in honeybees. *J. Exp. Biol.* 208 (20), 3895–3905.
- Banaei, M., et al., 2017. Walking through architectural spaces: the impact of interior forms on human brain dynamics. *Front. Hum. Neurosci.* 11 (417) <https://doi.org/10.3389/fnhum.2017.00477>.
- Banton, T., et al., 2005. The perception of walking speed in a virtual environment. *Presence* 14 (4), 394–406.
- Bar, M., et al., 2006. Top-down facilitation of visual recognition. *Proc. Natl. Acad. Sci. USA* 103 (2), 449–454. <https://doi.org/10.1073/pnas.0507062103>.
- Barrett, L.F., Bar, M., 2009. See it with feeling: affective predictions during object perception. *Philos. Trans. R. Soc. B: Biol. Sci.* 364 (1521), 1325–1334. <https://doi.org/10.1098/rstb.2008.0312>.
- Barsalou, L.W., 2008. Grounded cognition. *Annu. Rev. Psychol.* 59, 617–645. <https://doi.org/10.1146/annurev.psych.59.103006.093639>.
- Benedikt, M.L., 1979. To take hold of space: isovists and isovist fields. *Environ. Plan. B: Plan. Des.* 6 (1), 47–65. <https://doi.org/10.1068/b060047>.
- Benevento, L.A., Port, J.D., 1995. Single neurons with both form/color differential responses and saccade-related responses in the nonretinotopic pulvinar of the behaving macaque monkey. *Vis. Neurosci.* 2009/06/02, 12(3), pp. 523–544. doi: 10.1017/S0952523800008439.
- Bhagavatula, P.S., et al., 2011. Optic flow cues guide flight in birds. *Curr. Biol.* 21 (21), 1794–1799. <https://doi.org/10.1016/j.cub.2011.09.009>.
- Blanke, O., 2012. Multisensory brain mechanisms of bodily self-consciousness. *Nat. Rev. Neurosci.* 13 (8), 556–571. <https://doi.org/10.1038/nrn3292>.
- Blot, A., et al., 2021. Visual intracortical and transthalamic pathways carry distinct information to cortical areas. *Neuron* 109 (12), 1996–2008.e6. <https://doi.org/10.1016/j.neuron.2021.04.017>.
- Boly, M., et al., 2011. Preserved feedforward but impaired top-down processes in the vegetative state. *Y., N. Y. J.* 332 (6031), 858–862. <https://doi.org/10.1126/science.1202043>.
- Bremmer, F., Lappe, M., 1999. The use of optical velocities for distance discrimination and reproduction during visually simulated self motion. *Exp. Brain Res.* 127 (1), 33–42.
- Brown, H., et al., 2013. Active inference, sensory attenuation and illusions. *Cogn. Process.* 14 (4), 411–427. <https://doi.org/10.1007/s10339-013-0571-3>.
- Buffalo, E.A., et al., 2010. A backward progression of attentional effects in the ventral stream. *Proc. Natl. Acad. Sci. USA* 107 (1), 361–365. <https://doi.org/10.1073/pnas.0907658106>.
- Buffalo, E.A., et al., 2011. Laminar differences in gamma and alpha coherence in the ventral stream. *Proc. Natl. Acad. Sci.* 108 (27), 11262 LP–11211267. <https://doi.org/10.1073/pnas.1011284108>.
- Campana, F., et al., 2016. Conscious vision proceeds from global to local content in goal-directed tasks and spontaneous vision. *J. Neurosci.* 36 (19), 5200 LP–5205213 doi: 10.1523/JNEUROSCI.3619-15.2016.
- Carrasco, M., 2011. Visual attention: the past 25 years. *Vis. Res.* 51 (13), 1484–1525.
- Carrasco, M., Ling, S., Read, S., 2004. Attention alters appearance. *Nat. Neurosci.* 7 (3), 308–313. <https://doi.org/10.1038/nn1194>.
- Chaplin, T.A., Margrie, T.W., 2020. Cortical circuits for integration of self-motion and visual-motion signals. *Curr. Opin. Neurobiol.* 60, 122–128.
- Cisek, P., Kalaska, J.F., 2010. Neural mechanisms for interacting with a world full of action choices. *Annu. Rev. Neurosci.* 33 (1), 269–298. <https://doi.org/10.1146/annurev.neuro.051508.135409>.
- Clark, A., 2015. *Surfing Uncertainty: Prediction, Action and the embodied mind*. Oxford University Press, New York.
- Corcoran, A.W., Pezzulo, G., Hohwy, J., 2020. From allostatic agents to counterfactual cognisers: active inference, biological regulation, and the origins of cognition. *Biol. Philos.* 35 (3), 1–45.
- Dakin, R., Fellows, T.K., Altshuler, D.L., 2016. Visual guidance of forward flight in hummingbirds reveals control based on image features instead of pattern velocity. *Proc. Natl. Acad. Sci.* 113 (31), 8849 LP–8848854. <https://doi.org/10.1073/pnas.1603221113>.
- Damasio, A., 2010. *Self Comes to Mind*, First ed. Pantheon Books, New York.
- David, O., et al., 2006. Dynamic causal modeling of evoked responses in EEG and MEG. *NeuroImage* 30 (4), 1255–1272. <https://doi.org/10.1016/j.neuroimage.2005.10.045>.
- Dayan, P., et al., 1995. The helmholtz machine. *Neural Comput.* 7 (5), 889–904.
- De Jaegher, H., Di Paolo, E., Gallagher, S., 2010. Can social interaction constitute social cognition? *Trends Cogn. Sci.* 14 (10), 441–447. <https://doi.org/10.1016/j.tics.2010.06.009>.
- Dehaene, S., et al., 2001. Cerebral mechanisms of word masking and unconscious repetition priming. *Nat. Neurosci.* 4 (7), 752–758.
- Dehaene, S., et al., 2006. Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends Cogn. Sci.* 10 (5), 204–211. <https://doi.org/10.1016/j.tics.2006.03.007>.
- Di Paolo, E., Buhrmann, T., Barandiaran, X., 2017. *Sensorimotor life: an enactive proposal*. Oxford University Press.
- Djebbara, Z., et al., 2019. Sensorimotor brain dynamics reflect architectural affordances. *Proc. Natl. Acad. Sci. USA* 116 (29), 14769–14778. <https://doi.org/10.1073/pnas.1900648116>.
- Djebbara, Z., Fich, L.B., Gramann, K., 2021. The brain dynamics of architectural affordances during transition. *Sci. Rep.* 11 (1), 2796. <https://doi.org/10.1038/s41598-021-82504-w>.
- Do, T.-T.N., Lin, C.-T., Gramann, K., 2021. Human brain dynamics in active spatial navigation. *Sci. Rep.* 11 (1), 13036. <https://doi.org/10.1038/s41598-021-92246-4>.
- Dyhr, J.P., Higgins, C.M., 2010. The spatial frequency tuning of optic-flow-dependent behaviors in the bumblebee *Bombus impatiens*. *J. Exp. Biol.* 213 (10), 1643–1650. <https://doi.org/10.1242/jeb.041426>.
- Elman, J.L., 1990. Finding structure in time. *Cogn. Sci.* 14 (2), 179–211.
- Feldman, H., Friston, K.J., 2010. Attention, uncertainty, and free-energy. *Front. Hum. Neurosci.* 4. <https://doi.org/10.3389/fnhum.2010.00215>.
- Flament-Fultot, M., Nie, L., Carello, C., 2016. Perception-Action Mutuality Obviates Mental Construction. *Constr. Found.* 11 (2), 298–307 (Available at). <http://constr.uctivist.info/11/2/298.fultot>.
- Flint, A.C., Connors, B.W., 1996. Two types of network oscillations in neocortex mediated by distinct glutamate receptor subtypes and neuronal populations. *J. Neurophysiol.* 75 (2), 951–957. <https://doi.org/10.1152/jn.1996.75.2.951>.
- Foster, J.J., et al., 2017. Alpha-band oscillations enable spatially and temporally resolved tracking of covert spatial attention. *Psychol. Sci.* 28 (7), 929–941. <https://doi.org/10.1177/0956797617699167>.
- Foxe, J.J., Snyder, A.C., 2011. The role of alpha-band brain oscillations as a sensory suppression mechanism during selective attention. *Front. Psychol.* 2 (JUL) <https://doi.org/10.3389/fpsyg.2011.00154>.
- Fries, P., 2015. Rhythms for cognition: communication through coherence. *Neuron*. Cell Press 220–235. <https://doi.org/10.1016/j.neuron.2015.09.034>.
- Friston, K., 2005. A theory of cortical responses. *Philos. Trans. R. Soc. Lond. Ser. B, Biol. Sci.* 360 (1456), 815–836. <https://doi.org/10.1098/rstb.2005.1622>.
- Friston, K., 2010. The free-energy principle: a unified brain theory? *Nat. Rev. Neurosci.* 11 (2), 127–138. <https://doi.org/10.1038/nrn2787>.
- Friston, K., et al., 2017. Active inference: a process theory. *Neural Comput.* 29 (1), 1–49. [https://doi.org/10.1162/NECO\\_a.00912](https://doi.org/10.1162/NECO_a.00912).
- Friston, K., Kiebel, S., 2009. Predictive coding under the free-energy principle. *Philos. Trans. R. Soc. Lond. Ser. B, Biol. Sci.* 364 (1521), 1211–1221. <https://doi.org/10.1098/rstb.2008.0300>.
- Frith, C., 2009. *Making up the Mind: How the Brain Creates Our Mental World*. Wiley-Blackwell.
- Gallagher, S., 2017. *Enactivist interventions: rethinking the mind*, 1st ed. Oxford University Press, Oxford.
- Garrido, M.I., et al., 2008. The functional anatomy of the MMN: a DCM study of the roving paradigm. *NeuroImage* 2008/05/20, 42(2) 936–944. <https://doi.org/10.1016/j.neuroimage.2008.05.018>.
- Gehrke, L., Gramann, K., 2021. Single-trial regression of spatial exploration behavior indicates posterior EEG alpha modulation to reflect egocentric coding. *Eur. J. Neurosci.* 54 (12), 8318–8335. <https://doi.org/10.1111/ejn.15152>.
- Gibson, J., 1986. *The Ecological Approach to Visual Perception*. - Taylor & Francis Group. Psychology Press, East Sussex.
- Gibson, J.J., 1966. *The Senses Considered as Perceptual Systems*, 1st ed. Houghton Mifflin, Boston.
- Golesorkhi, M., Gomez-Pilar, J., Zilio, F., et al., 2021. The brain and its time: intrinsic neural timescales are key for input processing. *Commun. Biol.* 4 (1), 970. <https://doi.org/10.1038/s42003-021-02483-6>.
- Golesorkhi, M., Gomez-Pilar, J., Tumati, S., 2021. Temporal hierarchy of intrinsic neural timescales converges with spatial core-periphery organization. *Commun. Biol.* 4 (1), 1–14.
- Gramann, K., et al., 2011. Cognition in action: imaging brain/body dynamics in mobile humans. *Rev. Neurosci.* 22 (6), 593–608. <https://doi.org/10.1515/RNS.2011.047>.
- Gramann, K., et al., 2014. Imaging natural cognition in action. *Int. J. Psychophysiol.: Off. J. Int. Organ. Psychophysiol.* 91 (1), 22–29. <https://doi.org/10.1016/j.ijpsycho.2013.09.003>.
- Gramann, K., et al., 2021. Human cortical dynamics during full-body heading changes. *Sci. Rep.* 11 (1), 18186. <https://doi.org/10.1038/s41598-021-97749-8>.

- Guillery, R.W., 1995. Anatomical evidence concerning the role of the thalamus in corticocortical communication: a brief review. *J. Anat.* 187, 583–592 ( Pt 3(Pt 3)).
- Guillery, R.W., 2005. Anatomical pathways that link perception and action. *Prog. Brain Res.* 149, 235–256. [https://doi.org/10.1016/S0079-6123\(05\)49017-2](https://doi.org/10.1016/S0079-6123(05)49017-2).
- Halassa, M.M., Kastner, S., 2017. Thalamic functions in distributed cognitive control. *Nat. Neurosci.* 20 (12), 1669–1679. <https://doi.org/10.1038/s41593-017-0020-1>.
- Halgren, M., et al., 2019. The generation and propagation of the human alpha rhythm. *Proc. Natl. Acad. Sci.* 116 (47), 23772 LP–23723782. <https://doi.org/10.1073/pnas.1913092116>.
- Heft, H. (2020) 'Ecological Psychology and Enaction Theory: Divergent Groundings', *Frontiers in Psychology*. Available at: <https://www.frontiersin.org/article/10.3389/fpsyg.2020.00991>.
- Hillier, B., Hanson, J., 1989. *The social logic of space*. Cambridge university press.
- Hillyard, S.A., Vogel, E.K., Luck, S.J., 1998. Sensory gain control (amplification) as a mechanism of selective attention: electrophysiological and neuroimaging evidence'. In: Humphreys, G.W., Duncan, J., Treisman, A. (Eds.), *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 353, pp. 1257–1270. <https://doi.org/10.1098/rstb.1998.0281>.
- Hochstein, S., Ahissar, M., 2002. View from the top: hierarchies and reverse hierarchies in the visual system. *Neuron* 36 (5), 791–804. [https://doi.org/10.1016/S0896-6273\(02\)01091-7](https://doi.org/10.1016/S0896-6273(02)01091-7).
- Hohwy, J., 2013. *The Predictive Mind*, First ed. Oxford University Press, Oxford. <https://doi.org/10.1093/acprof:oso/9780199682737.001.0001>.
- Hölle, D., Meekes, J., Bleichner, M.G., 2021. Mobile ear-EEG to study auditory attention in everyday life: Auditory attention in everyday life. *Behav. Res. Methods* 53 (5), 2025–2036. <https://doi.org/10.3758/s13428-021-01538-0>.
- Itti, L., Baldi, P., 2009. Bayesian surprise attracts human attention. *Vis. Res.* 49 (10), 1295–1306.
- Javadi, A.-H., et al., 2017. Hippocampal and prefrontal processing of network topology to simulate the future. *Nat. Commun.* 8 (1), 14652. <https://doi.org/10.1038/ncomms14652>.
- Jiang, J., Summerfield, C., Egner, T., 2013. Attention sharpens the distinction between expected and unexpected percepts in the visual brain. *J. Neurosci.* 33 (47), 18438 LP–18418447. <https://doi.org/10.1523/JNEUROSCI.3308-13.2013>.
- Kanai, R., et al., 2015. Cerebral hierarchies: predictive processing, precision and the pulvinar. *Philos. Trans. R. Soc. B: Biol. Sci.* 370 (1668), 20140169.
- Kastner, S., Fiebelkorn, I.C., Eradath, M.K., 2020. Dynamic pulvino-cortical interactions in the primate attention network. *Curr. Opin. Neurobiol.* 65, 10–19. <https://doi.org/10.1016/j.conb.2020.08.002>.
- Keller, G.B., Bonhoeffer, T., Hübener, M., 2012. Sensorimotor mismatch signals in primary visual cortex of the behaving mouse. *Neuron* 74 (5), 809–815.
- Khan, A.G., Hofer, S.B., 2018. Contextual signals in visual cortex. *Curr. Opin. Neurobiol.* 52, 131–138.
- Klimesch, W., 1997. EEG-alpha Rhythms and Memory Processes. *International Journal of Psychophysiology*. Elsevier, pp. 319–340. [https://doi.org/10.1016/S0167-8760\(97\)00773-3](https://doi.org/10.1016/S0167-8760(97)00773-3).
- Klimesch, W., 2012. Alpha-band oscillations, attention, and controlled access to stored information. *Trends Cogn. Sci.* 606–617. <https://doi.org/10.1016/j.tics.2012.10.007>.
- Klug, M., Gramann, K., 2021. Identifying key factors for improving ICA-based decomposition of EEG data in mobile and stationary experiments. *Eur. J. Neurosci.* 54 (12), 8406–8420. <https://doi.org/10.1111/ejn.14992>.
- Komura, Y., et al., 2013. Responses of pulvino neurons reflect a subject's confidence in visual categorization. *Nat. Neurosci.* 16 (6), 749–755. <https://doi.org/10.1038/nn.3393>.
- Lachaux, J.P., et al., 1999. Measuring phase synchrony in brain signals. *Hum. Brain Mapp.* 8 (4), 194–208. [https://doi.org/10.1002/\(SICI\)1097-0193\(1999\)8:4<194::AID-HBM4>3.0.CO;2-C](https://doi.org/10.1002/(SICI)1097-0193(1999)8:4<194::AID-HBM4>3.0.CO;2-C).
- Lamontagne, A., et al., 2007. Modulation of walking speed by changing optic flow in persons with stroke. *J. Neuroeng. Rehabil.* 4 (1), 1–8.
- Lennie, P., 2003. The cost of cortical computation. *Curr. Biol.* 13 (6), 493–497.
- Leonards, U., et al., 2015. Treacherous pavements: paving slab patterns modify intended walking directions (Available at). *PLOS ONE* 10 (6), e0130034. <https://doi.org/10.1371/journal.pone.0130034>.
- Limanowski, J., Friston, K., 2020. Attentional modulation of vision versus proprioception during action. *Cereb. Cortex* (N. Y., N. Y.: 1991), 30(3) 1637–1648. <https://doi.org/10.1093/cercor/bhz192>.
- Llinás, R., et al., 1998. The neuronal basis for consciousness. *Philos. Trans. R. Soc. B: Biol. Sci. R. Soc.* 1841–1849. <https://doi.org/10.1098/rstb.1998.0336>.
- Llinás, R., et al., 2005. Rhythmic and dysrhythmic thalamocortical dynamics: GABA systems and the edge effect. *Trends in Neurosciences*. Elsevier Ltd, pp. 325–333. <https://doi.org/10.1016/j.tins.2005.04.006>.
- Ludwig, C.J.H., et al., 2018. The influence of visual flow and perceptual load on locomotion speed. *Atten., Percept. Psychophys.* 80 (1), 69–81. <https://doi.org/10.3758/s13414-017-1417-3>.
- Makeig, S., et al., 2009. Linking brain, mind and behavior. *Int. J. Psychophysiol.* 73 (2), 95–100. <https://doi.org/10.1016/J.IJPSYCHO.2008.11.008>.
- Manser, M.P., Hancock, P.A., 2007. The influence of perceptual speed regulation on speed perception, choice, and control: tunnel wall characteristics and influences. *Accid. ; Anal. Prev.* 39 (1), 69–78. <https://doi.org/10.1016/j.aap.2006.06.005>.
- Marois, R., Yi, D.-J., Chun, M.M., 2004. The neural fate of consciously perceived and missed events in the attentional blink. *Neuron* 41 (3), 465–472.
- Martínez-Trujillo, J.C., Treue, S., 2002. Attentional modulation strength in cortical area MT depends on stimulus contrast. *Neuron* 35 (2), 365–370. [https://doi.org/10.1016/S0896-6273\(02\)00778-X](https://doi.org/10.1016/S0896-6273(02)00778-X).
- Maturana, H.R., Varela, F.J., 1992. *The tree of knowledge: the biological roots of human understanding*, First ed. Shambhala, Boston.
- Maunsell, J.H.R., 2015. Neuronal mechanisms of visual attention. *Annu. Rev. Vis. Sci.* 1, 373–391.
- McAdams, C.J., Maunsell, J.H.R., 1999. Effects of attention on the reliability of individual neurons in monkey visual cortex. *Neuron* 23 (4), 765–773. [https://doi.org/10.1016/S0896-6273\(01\)80034-9](https://doi.org/10.1016/S0896-6273(01)80034-9).
- Mease, R.A., Gonzalez, A.J., 2021. Corticothalamic pathways from layer 5: emerging roles in computation and pathology. *Front. Neural Circuit.* 88. Available at: <https://www.frontiersin.org/article/10.3389/fncir.2021.730211>.
- Miller, M., Rietveld, E., Kiverstein, J., 2021. The predictive dynamics of happiness and well-being. *17540739211063852 Emot. Rev.* <https://doi.org/10.1177/17540739211063851>.
- Mitchell, A.S., et al., 2014. Advances in understanding mechanisms of thalamic relays in cognition and behavior. *J. Neurosci.* 34 (46), 15340–15346.
- Mitchell, A.S., 2015. The mediodorsal thalamus as a higher order thalamic relay nucleus important for learning and decision-making. *Neurosci. Biobehav. Rev.* 54, 76–88. <https://doi.org/10.1016/j.neubiorev.2015.03.001>.
- Mitchell, A.S., Chakraborty, S., 2013. What does the mediodorsal thalamus do? *Front. Syst. Neurosci.* 7, 37.
- Mo, C., Sherman, S.M., 2019. A sensorimotor pathway via higher-order thalamus. *J. Neurosci.* 39 (4), 692 LP–692704. <https://doi.org/10.1523/JNEUROSCI.1467-18.2018>.
- Mohler, B.J., et al., 2004. Visual motion influences locomotion in a treadmill virtual environment. *Proc. 1st Symp. Appl. Percept. Graph. Vis.* 19–22.
- Moore, B., et al., 2019. Cortical projections to the two retinotopic maps of primate pulvino are distinct. *J. Comp. Neurol.* 527 (3), 577–588. <https://doi.org/10.1002/cne.24515>.
- Moutoussis, K., Zeki, S., 2002. The relationship between cortical activation and perception investigated with invisible stimuli. *Proc. Natl. Acad. Sci.* 99 (14), 9527–9532.
- Mukherjee, A., et al., 2020. Variation of connectivity across exemplar sensory and associative thalamocortical loops in the mouse. In: Colgin, L.L., et al. (Eds.), *eLife*, 9. <https://doi.org/10.7554/eLife.62554>.
- Mukherjee, A., et al., 2021. Thalamic circuits for independent control of prefrontal signal and noise. *Nature*. <https://doi.org/10.1038/s41586-021-04056-3>.
- Mullen, T.R., et al., 2015. Real-time neuroimaging and cognitive monitoring using wearable dry EEG. *IEEE Trans. Bio-Med. Eng.* 2015/09/23 62 (11), 2553–2567. <https://doi.org/10.1109/TBME.2015.2481482>.
- Mumford, D., 1992. On the computational architecture of the neocortex. *Biol. Cybern.* 66 (3), 241–251.
- Newen, A., De Bruin, L., Gallagher, S. (Eds.), 2018. *The Oxford Handbook of 4E Cognition*. Oxford University Press. <https://doi.org/10.1093/oxfordhb/9780198735410.001.0001>.
- Niell, C.M., Stryker, M.P., 2010. Modulation of visual responses by behavioral state in mouse visual cortex. *Neuron* 65 (4), 472–479.
- Northoff, G., 2018. *The Spontaneous Brain: From the Mind-Body to the World-Brain Problem*. MIT Press, Cambridge, Mass.
- Northoff, G., Huang, Z., 2017. How do the brain's time and space mediate consciousness and its different dimensions? Temporo-spatial theory of consciousness (TTC). *Neurosci. Biobehav. Rev.* 80, 630–645. <https://doi.org/10.1016/j.neubiorev.2017.07.013>.
- Northoff, G., Wainio-Theberge, S., Evers, K., 2019. Is temporo-spatial dynamics the "common currency" of brain and mind? In *Quest of "Spatiotemporal Neuroscience*. *Physics of Life Reviews*. Elsevier B.V. <https://doi.org/10.1016/j.plrev.2019.05.002>.
- O'Regan, K., Noë, A., 2001a. A sensorimotor account of vision and visual consciousness. *Behav. Brain Sci.* 24 (5), 939–1031.
- O'Regan, K., Noë, A., 2001b. What it is like to see: a sensorimotor theory of perceptual experience. *Synthese* 129 (1), 79–103. <https://doi.org/10.1023/A:1012699224677>.
- Palmer, C.R., Kristan, W.B., 2011. Contextual modulation of behavioral choice. *Curr. Opin. Neurobiol.* 21 (4), 520–526. <https://doi.org/10.1016/j.conb.2011.05.003>.
- Parada, F.J., 2018. Understanding natural cognition in everyday settings: 3 pressing challenges. *Front. Hum. Neurosci.* 12, 386. <https://doi.org/10.3389/fnhum.2018.00386>.
- Pechtl, K.S., Jennings, J.R., Redfern, M.S., 2020. Optic flow and attention alter locomotion differently in the young and old. *Gait Posture* 76, 1–6. <https://doi.org/10.1016/j.gaitpost.2019.10.022>.
- Pezzulo, G., Cisek, P., 2016. Navigating the affordance landscape: feedback control as a process model of behavior and cognition. *Trends Cogn. Sci.* 20 (6), 414–424. <https://doi.org/10.1016/j.tics.2016.03.013>.
- Phillips, I., Block, N., 2017. Debate on unconscious perception. In *Current controversies in philosophy of perception*. Routledge, pp. 165–192.
- Pickincke, J., Chien, J.H., Mukherjee, M., 2014. Varying the speed of perceived self-motion affects postural control during locomotion. *Stud. Health Technol. Inform.* 196, 319–324.
- Posner, M.I., Snyder, C.R., Davidson, B.J., 1980. Attention and the detection of signals. *Journal of Experimental Psychology: General*. US: American Psychological Association, pp. 160–174 doi: 10.1037/0096-3445.109.2.160.
- Prokop, T., Schubert, M., Berger, W., 1997. Visual influence on human locomotion modulation to changes in optic flow. *Exp. Brain Res.* 114 (1), 63–70. <https://doi.org/10.1007/PL00005624>.
- Purushothaman, G., et al., 2012. Gating and control of primary visual cortex by pulvino. *Nat. Neurosci.* 15 (6), 905–912.
- Rakha, H.A., Katz, B.J., Duke, D., 2006. Design and evaluation of peripheral transverse bars to reduce vehicle speed. *Environ. Sci.*

- Rao, R.P.N., Ballard, D.H., 1999. Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. *Nat. Neurosci.* 2 (1), 79–87. <https://doi.org/10.1038/4580>.
- Read, C., Szokolszky, A., 2020. Ecological psychology and enactivism: perceptually-guided action vs. sensation-based enaction. *Front. Psychol.* Available at: <https://www.frontiersin.org/article/10.3389/fpsyg.2020.01270>.
- Reynolds, J.H., Pasternak, T., Desimone, R., 2000. Attention increases sensitivity of V4 neurons. *Neuron* 26 (3), 703–714. [https://doi.org/10.1016/S0896-6273\(00\)81206-4](https://doi.org/10.1016/S0896-6273(00)81206-4).
- Richter, C.G., et al., 2017. Phase-amplitude coupling at the organism level: the amplitude of spontaneous alpha rhythm fluctuations varies with the phase of the infra-slow gastric basal rhythm. *NeuroImage* 146, 951–958. <https://doi.org/10.1016/j.neuroimage.2016.08.043>.
- Rojas-Libano, D., Parada, F.J., 2020. Body-world coupling, sensorimotor mechanisms, and the ontogeny of social cognition. *Front. Psychol.*
- Romo, R., Lemus, L., de Lafuente, V., 2012. Sense, memory, and decision-making in the somatosensory cortical network. *Curr. Opin. Neurobiol.* 22 (6), 914–919. <https://doi.org/10.1016/j.conb.2012.08.002>.
- Roth, M.M., et al., 2016. Thalamic nuclei convey diverse contextual information to layer 1 of visual cortex. *Nat. Neurosci.* 19 (2), 299–307. <https://doi.org/10.1038/nn.4197>.
- Rouiller, E.M., Welker, E., 2000. A comparative analysis of the morphology of corticothalamic projections in mammals. *Brain Res. Bull.* 53 (6), 727–741.
- Ryle, G., 1945. Knowing how and knowing that: the presidential address. *Proc. Aristot. Soc.* 46, 1–16.
- Saalmann, Y.B., et al., 2012. The pulvinar regulates information transmission between cortical areas based on attention demands. *Sci. (N. Y., N. Y.)* 337 (6095), 753–756. <https://doi.org/10.1126/science.1223082>.
- Saalmann, Y.B., Kastner, S., 2009. Gain control in the visual thalamus during perception and cognition. *Curr. Opin. Neurobiol.* 19 (4), 408–414. <https://doi.org/10.1016/j.conb.2009.05.007>.
- Saleem, A.B., et al., 2013. Integration of visual motion and locomotion in mouse visual cortex. *Nat. Neurosci.* 16 (12), 1864–1869.
- Salomon, R., et al., 2016. The insula mediates access to awareness of visual stimuli presented synchronously to the heartbeat. *J. Neurosci.: Off. J. Soc. Neurosci.* 36 (18), 5115–5127. <https://doi.org/10.1523/JNEUROSCI.4262-15.2016>.
- Seeber, M., et al., 2019. Subcortical electrophysiological activity is detectable with high-density EEG source imaging. *Nat. Commun.* 10 (1), 753. <https://doi.org/10.1038/s41467-019-08725-w>.
- Sergent, C., Baillet, S., Dehaene, S., 2005. Timing of the brain events underlying access to consciousness during the attentional blink. *Nat. Neurosci.* 8 (10), 1391–1400.
- Seth, A.K., 2014. A predictive processing theory of sensorimotor contingencies: Explaining the puzzle of perceptual presence and its absence in synesthesia. *Cogn. Neurosci.* 5 (2), 97–118. <https://doi.org/10.1080/17588928.2013.877880>.
- Seymour, R.A., et al., 2021. Using OPMs to measure neural activity in standing, mobile participants. *NeuroImage* 244, 118604. <https://doi.org/10.1016/j.neuroimage.2021.118604>.
- Seymour, R.A., et al., 2022. Interference suppression techniques for OPM-based MEG: Opportunities and challenges. *NeuroImage* 247, 118834. <https://doi.org/10.1016/j.neuroimage.2021.118834>.
- Sherman, M.T., et al., 2015. Prior expectations facilitate metacognition for perceptual decision. *Conscious. Cogn.* 35, 53–65. <https://doi.org/10.1016/j.concog.2015.04.015>.
- Sherman, S.M., Guillery, R.W., 1996. Functional organization of thalamocortical relays. *J. Neurophysiol.* 76 (3), 1367–1395. <https://doi.org/10.1152/jn.1996.76.3.1367>.
- Sherman, S.M., Guillery, R.W., 1998. On the actions that one nerve cell can have on another: distinguishing “drivers” from “modulators”. *Proc. Natl. Acad. Sci.* 95 (12), 7121 LP–7127126. <https://doi.org/10.1073/pnas.95.12.7121>.
- Sherman, S.M., Guillery, R.W., 2002. The role of the thalamus in the flow of information to the cortex. *Philos. Trans. R. Soc. Lond. Ser. B, Biol. Sci.* 357 (1428), 1695–1708. <https://doi.org/10.1098/rstb.2002.1161>.
- Sherman, S.M., Guillery, R.W., 2006. Exploring the thalamus and its role in cortical function. MIT press.
- Sherman, S.M., Guillery, R.W., 2011. Distinct functions for direct and transthalamic corticocortical connections. *J. Neurophysiol.* 106 (3), 1068–1077. <https://doi.org/10.1152/jn.00429.2011>.
- Sherman, S.M., Guillery, R.W., 2013. Functional connections of cortical areas: a new view from the thalamus. MIT Press.
- Sherman, S.M., Usrey, W.M., 2021. Cortical control of behavior and attention from an evolutionary perspective. *Neuron* 109 (19), 3048–3054. <https://doi.org/10.1016/j.neuron.2021.06.021>.
- Shipp, S., 2003. The functional logic of cortico-pulvinar connections. *Philos. Trans. R. Soc. Lond. Ser. B, Biol. Sci.* 358 (1438), 1605–1624. <https://doi.org/10.1098/rstb.2002.1213>.
- Shipp, S., 2005. The importance of being agranular: a comparative account of visual and motor cortex. *Philos. Trans. R. Soc. B: Biol. Sci.* 360 (1456), 797–814. <https://doi.org/10.1098/rstb.2005.1630>.
- Shipp, S., 2007. Structure and function of the cerebral cortex. *Curr. Biol.* 17 (12), R443–R449.
- Silva, L.R., Amitai, Y., Connors, B.W., 1991. Intrinsic oscillations of neocortex generated by layer 5 pyramidal neurons. *Science* 251 (4992), 432 LP–432435. <https://doi.org/10.1126/science.1824881>.
- Simmel, G., 1995. *Metropolis and Mental Life*. In: Kasinitz, P. (Ed.), *Metropolis: Center and Symbol of Our Times*. NYU Press, New York.
- Smout, C.A., et al., 2019. ‘Attention promotes the neural encoding of prediction errors’. In: Seymour, B. (Ed.), *PLOS Biology*, 17. <https://doi.org/10.1371/journal.pbio.2006812>.
- Spaak, E., et al., 2012. Layer-specific entrainment of gamma-band neural activity by the alpha rhythm in monkey visual cortex. *Curr. Biol.* 22 (24), 2313–2318. <https://doi.org/10.1016/j.cub.2012.10.020>.
- Srinivasan, M., et al., 1996. Honeybee navigation en route to the goal: visual flight control and odometry. *J. Exp. Biol.* 199 (1), 237–244.
- Stamps, A.E., 2005. Isovists, enclosure, and permeability theory. *Environ. Plan. B: Plan. Des.* 32 (5), 735–762. <https://doi.org/10.1068/b31138>.
- Steriade, M., et al., 1990. Basic mechanisms of cerebral rhythmic activities. *Electroencephalogr. Clin. Neurophysiol.* 76 (6), 481–508. [https://doi.org/10.1016/0013-4694\(90\)90001-Z](https://doi.org/10.1016/0013-4694(90)90001-Z).
- Thaler, R., Sunstein, C., 2021. *Nudge*. Final Edit. Penguin Books, US.
- Thompson, E., 2005. Sensorimotor Subjectivity and the Enactive Approach to Experience. *Phenomenology and the Cognitive Sciences*. Springer, pp. 407–427. <https://doi.org/10.1007/s11097-005-9003-x>.
- Thompson, E., 2007. *Mind in life: biology, phenomenology, and the sciences of mind*, First ed. Belknap Press of Harvard University Press, London, England.
- Thompson, E., Varela, F.J., 2001. Radical embodiment: neural dynamics and consciousness. *Trends Cogn. Sci.* 5 (10), 418–425. [https://doi.org/10.1016/S1364-6613\(00\)01750-2](https://doi.org/10.1016/S1364-6613(00)01750-2).
- Van de Cruys, S., 2017. Affective value in the predictive mind. *Philos. Predict. Process.* 1–21. <https://doi.org/10.15502/9783958573253>.
- van Wijk, B.C.M., 2018. Generic dynamic causal modelling: an illustrative application to Parkinson’s disease. *NeuroImage* 181, 818–830. <https://doi.org/10.1016/j.neuroimage.2018.08.039>.
- Varela, F., et al., 2001. The brainweb: phase synchronization and large-scale integration. *Nat. Rev. Neurosci.* 2 (4), 229–239. <https://doi.org/10.1038/35067550>.
- Varela, F.G., Maturana, H.R., Uribe, R., 1974. Autopoiesis: the organization of living systems, its characterization and a model. *Biosystems* 5 (4), 187–196. [https://doi.org/10.1016/0303-2647\(74\)90031-8](https://doi.org/10.1016/0303-2647(74)90031-8).
- Varela, F.J., Thompson, E., Rosch, E., 2016. *The Embodied Mind: Cognitive Science and Human Experience*. Revised ed. MIT Press, London, England.
- Villeneuve, M.Y., et al., 2005. Pattern–motion selectivity in the human pulvinar. *NeuroImage* 28 (2), 474–480. <https://doi.org/10.1016/j.neuroimage.2005.06.015>.
- Villeneuve, M.Y., et al., 2012. Pattern-motion selective responses in MT, MST and the pulvinar of humans. *Eur. J. Neurosci.* 36 (6), 2849–2858. <https://doi.org/10.1111/j.1460-9568.2012.08205.x>.
- Vuilleumier, P., et al., 2001. Neural fate of seen and unseen faces in visuospatial neglect: a combined event-related functional MRI and event-related potential study. *Proc. Natl. Acad. Sci.* 98 (6), 3495–3500.
- Ward, L.M., 2013. The thalamus: gateway to the mind. *Wiley Interdiscip. Rev. Cogn. Sci.* 4 (6), 609–622. <https://doi.org/10.1002/wcs.1256>.
- Wiener, J.M., et al., 2007. Isovist analysis captures properties of space relevant for locomotion and experience. *Perception* 36 (7), 1066–1083. <https://doi.org/10.1068/p5587>.
- Wilkins, A.J., Penacchio, O., Leonards, U., 2018. The built environment and its patterns: a view from the vision sciences. *J. Sustain. Des. Appl. Res.* 6 (1).
- Wolff, A., et al., 2022. Intrinsic neural timescales: temporal integration and segregation. *Trends Cogn. Sci.*
- Wolff, M., et al., 2020. A thalamic bridge from sensory perception to cognition. *Neurosci. Biobehav. Rev.* <https://doi.org/10.1016/j.neubiorev.2020.11.013>.
- Wunderlich, A., Gramann, K., 2021. Landmark-based navigation instructions improve incidental spatial knowledge acquisition in real-world environments. *J. Environ. Psychol.* 77, 101677. <https://doi.org/10.1016/j.jenvp.2021.101677>.
- Zhou, H., Schafer, R.J., Desimone, R., 2016. Pulvinar-cortex interactions in vision and attention. *Neuron* 89 (1), 209–220.