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***The conceptual framework of information  
processing in action***

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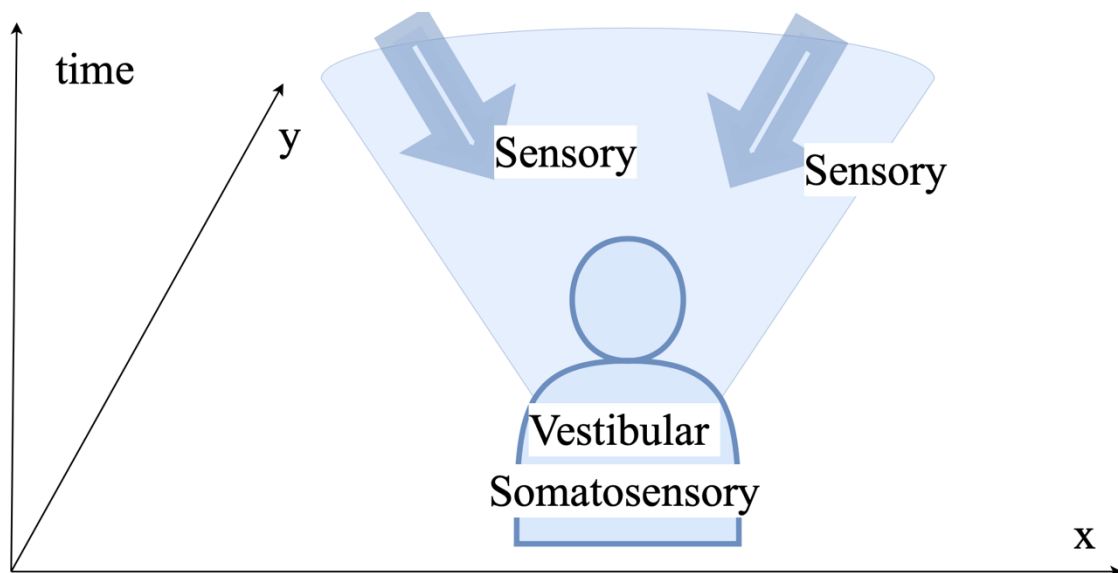
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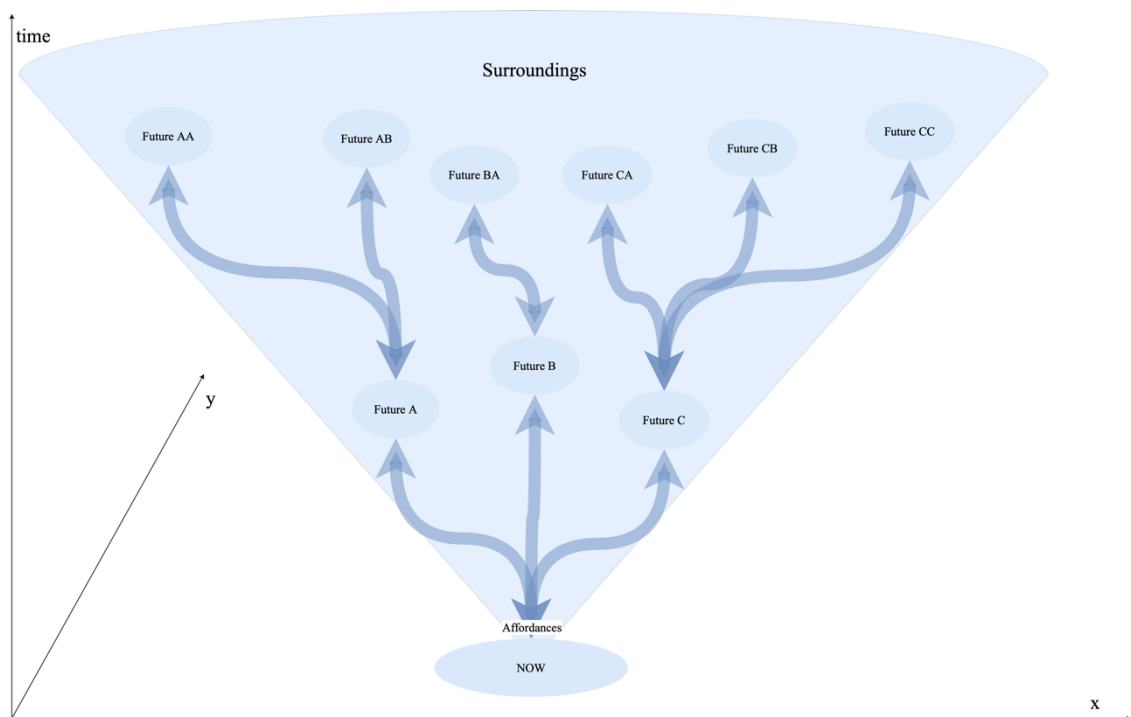
## Introduction

This work begins with the claim that animals fundamentally process physical, chemical, and biological information (Oyama, 2000). Information can be understood in many ways, such as a DNA code, action potentials propagated from the sensory receptors or activity of the large-scale brain networks. Information is thus a capacious term that is further operationalized into three information channels. Sensory information involves information "from the outside"; somatosensory information involves information about the state of the body, while vestibular information reflects the body's locomotion (**Figure 1**). For example, sensory information includes chemical information attracting and repelling simple organisms or visual information reaching the human eye (Milner, 2017). Somatosensory information, on the other hand, provides information such as piercing a single cell's membrane or the skin's temperature (ten Donkelaar et al., 2020), while vestibular information encloses gravitational information about a change in velocity (acceleration/deceleration) and angular momentum of the head (Day & Fitzpatrick, 2005). It is claimed here that the necessary and sufficient conditions for describing a biological body acting in the physical space are to treat it as a system processing sensory, somatosensory, and vestibular information.



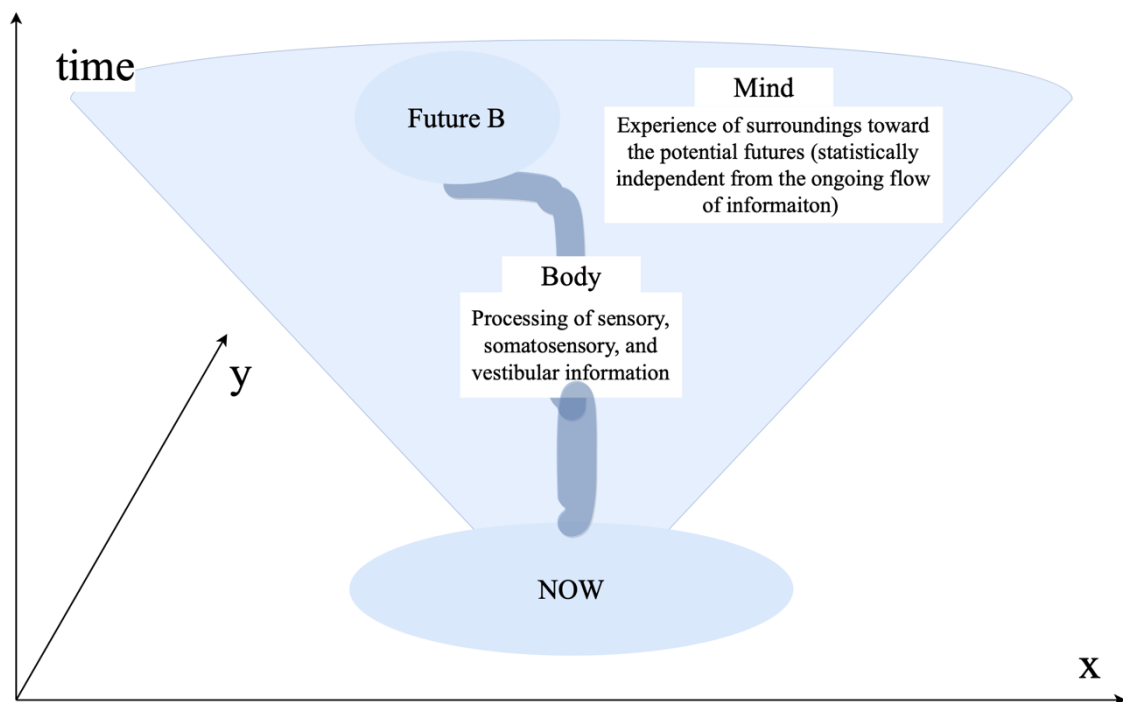
**Figure 1. The biological body in the physical space is fully described with sensory, somatosensory, and vestibular information.** Sensory information is smell, hearing, and vision; somatosensory information is pain, pressure, temperature, and proprioception through stimulating muscles and joints; vestibular information is spatial orientation. The flow of information in these channels fully characterizes the biological body acting in the physical space.

Nevertheless, it should be observed that understanding living beings in terms of information processing systems ignores the everyday phenomenological experience even though we experience qualia, not information processing per se. To address this gap, a phenomenological experience specific to action will be analyzed. The action-oriented qualia are experienced as affordances - possibilities for action that lead to the plurality of hierarchically organized potential futures. The rich landscape of affordances is called here the **surroundings**, which reflects Gibson’s (2014a) understanding of the term environment and Levontin’s (2000) understanding of the term niche (**Figure 2**). The surroundings thus encompass the experience of the potential futures, such as locomotion or reaching an object, and much thicker in time actions such as finishing a book or contributing to the civilizational goals. The temporal thickness of an organism depends on its phylogeny and ontogeny, encapsulating the entirety of the organism’s history (Friston, 2018). Taking action toward a specific future thus entails following affordances experienced as leading toward this future.



**Figure 2. Phenomenological surroundings of multiple potential futures.** At its current state (now), an organism experiences possibilities for actions toward possible ends known as affordances. These action-oriented qualia are hierarchically organized paths toward the future constituting the surroundings (rich landscape of affordances). Humans have the most robust temporal thickness (“cognitive light cone”) that can reach even beyond their lifespan, i.e., people are capable of experiencing the distant future and acting upon it.

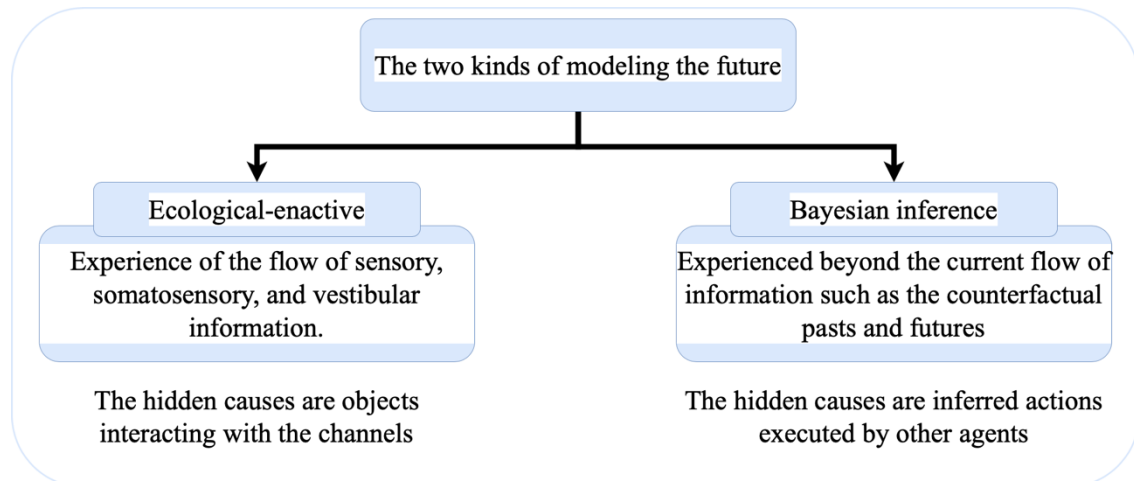
The discrepancy between processing the information in the biological system and an organism’s phenomenological experience is known as the mind-body problem (J. R. Anderson, 2007; Frith, 2007; Wiese & Friston, 2021). It implies that at some point in the phylogeny, the experience of affordances became a proxy for balancing the information toward the potential futures (**Figure 3**). In the case of humans, the conscious experience is statistically independent of the flow of sensory, somatosensory, and vestibular information and arises from the information processing in the posteriorly located set of brain areas known as “gestalt areas” (Dehaene & Changeux, 2011; Lieberman, 2022; Tononi & Koch, 2015). This idea relates to the distinction between the “remembering self” that remembers and plans the future and the “experiencing self” actually living life (Kahneman & Riis, 2005; Zajchowski et al., 2017). Sensory, somatosensory, and vestibular information propagated to the gestalt areas results in experiencing the physical world. In contrast, information dissociated from these inputs that reach the gestalt areas results in experiencing the affordances toward the more distal futures “in mind”.



**Figure 3. Experience of surroundings.** Potential futures are experienced with affordances. Once affordances are followed, they correspond to the specific flows of information in the sensory, somatosensory, and vestibular channels. The experience is computed in the gestalt areas that receive information varyingly correlated with the ongoing flow of sensory, somatosensory, and vestibular inputs.

The experience of action-oriented qualia processed by the gestalt areas includes the immediate and the far future. This conscious experience of surroundings is composed

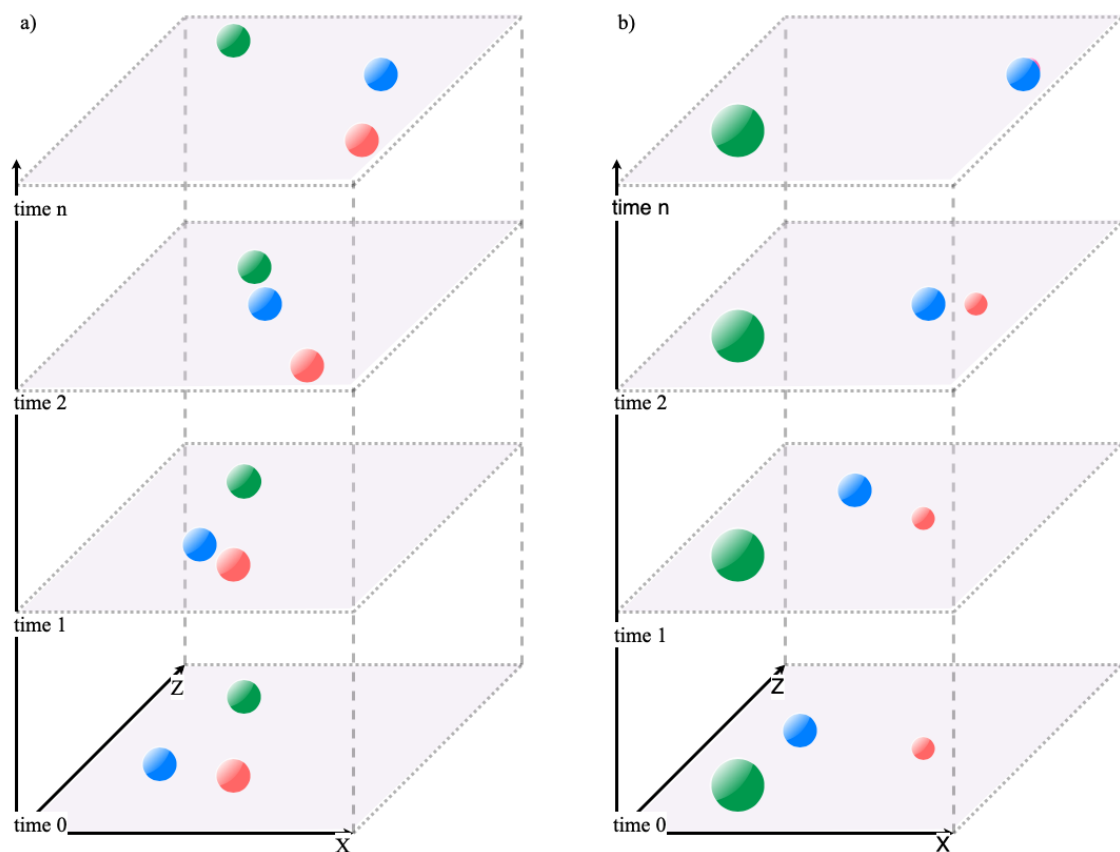
of two models: (I) the ecological-enactive model connected with the ongoing flow of information from the biological body processing physical space and (II) the Bayesian model dissociated from this flow (Bruineberg, Kiverstein, et al., 2018; Constant et al., 2021) (**Figure 4**). Here, these models are interpreted as biomechanical and inferred spaces computed with specialized brain networks that become conscious when coupled with the gestalt areas. The spaces are composed of information already transduced from the receptors and along the nervous system; thus, the spaces are *representational*. On the one hand, representations are directly coupled with the ongoing stream of the incoming information (i.e., perceiving representations of the encountered physical world); on the other hand, representations are decoupled from this information and denote latent causes behind the incoming information. In addition, the spaces are investigated in psychology and neuroscience as memory systems, which in advanced organisms are divided into “procedural”, and “declarative” (Poldrack & Packard, 2003a; Squire, 2004; Ullman, 2016). The procedural memory makes associations within the ongoing flow of information, while the declarative memory makes interdimensional associations (Hikosaka et al., 1999; Keele et al., 2003). The architecture of information processing behind the memory systems reveal the insights about organization of the brain networks.



**Figure 4. Two models for the future.** Experience of surroundings originates from highly processed information entering the gestalt areas. Thus, the entirety of the experience is representational. The content for the sake of action involves experiencing the actual flow of information (e.g., driving a car) or being dissociated from it (e.g., planning a business meeting while driving a car). The latter case is exemplified as an inference about the intentional states of other agents that compose the social world.

A biological body in the physical space can be described in terms of exchanging kinetic and potential energies in the biomechanical space (Knudson, 2021) (**Figure 5a**). The dimensions of the biomechanical space are enclosed in the sensory, somatosensory,

and vestibular information. Complementary, the dimensions of the inferred space are enclosed in agents' social interactions (Gollwitzer, 1999; Pacherie, 2008; Tomasello, 2018) (**Figure 5b**). The brain networks that compute the two spaces train each other in organism's ontogeny (M. Chen et al., 2022). The action-oriented experience of the surroundings is mediated by the "control" network that partially overlaps with the gestalt areas (Uddin et al., 2019), and gates the access of the networks calculating the biomechanical and inferred n-dimensional spaces to the gestalt areas (Dixon et al., 2018). The creation of the inferred space has been experimentally investigated in research on the Theory of Mind (J. R. Anderson et al., 2004; Frith, 2007; H. L. Gallagher & Frith, 2003; Goel et al., 1995).



**Figure 5. Objects and agents exchange information in time.** The x and z axes denote the position in the space of information exchange. **a)** Example of the billiard balls exchanging kinetic and potential energies in the physical space. **b)** Example of a stationary agent (green), a predator (blue), and a prey (red) exchanging information in the n-dimensional inferred space. The dimensions of the latter space depend on the interactions between the agents that are modeled with their potential future actions (e.g., how agile other agents are).

The information processing behind the experience of the surroundings involves simultaneous and independent encoding and retrieval of the biomechanical and inferred spaces in the respective networks. Such simultaneous and independent information processing is identified in multiple dual theories of memory developed in psychology and neuroscience (Dolan & Dayan, 2013; Geerts et al., 2020a; Poldrack & Packard, 2003a; Squire, 1992). Here, these insights are reviewed in light of the large-scale brain networks that underpin the experience by processing information in a highly organized way (M. Chen et al., 2022; Dixon et al., 2018; C. Murphy et al., 2018; Uddin et al., 2019). The phylogenetic and ontogenetic interactions between the networks constitute the information flow in the entire system. To explore the organization of the information processing system in detail, three principles governing information processing are postulated:

- Information processing is **distributed**.
- Information processing is **future-oriented**.
- Information processing is **memory-guided**.

The idea of **distributed information processing** has emerged in anthropology with the recognition of the social aspects of human cognition, presented by Vygotsky and Cole (1978), and Minsky (1988). Later, Hutchins (2000) distinguished at least three types of distributed information processing. Firstly, information processing is often distributed among members of a social group. Secondly, information processing requires the animal to coordinate the internal and external states. Lastly, earlier events can impact later events, resulting in the distribution of processes through time (Hutchins, 2000). Put simply, the distribution of the information processing systems means that the systems enclose physical objects and social agents and are embedded in time.

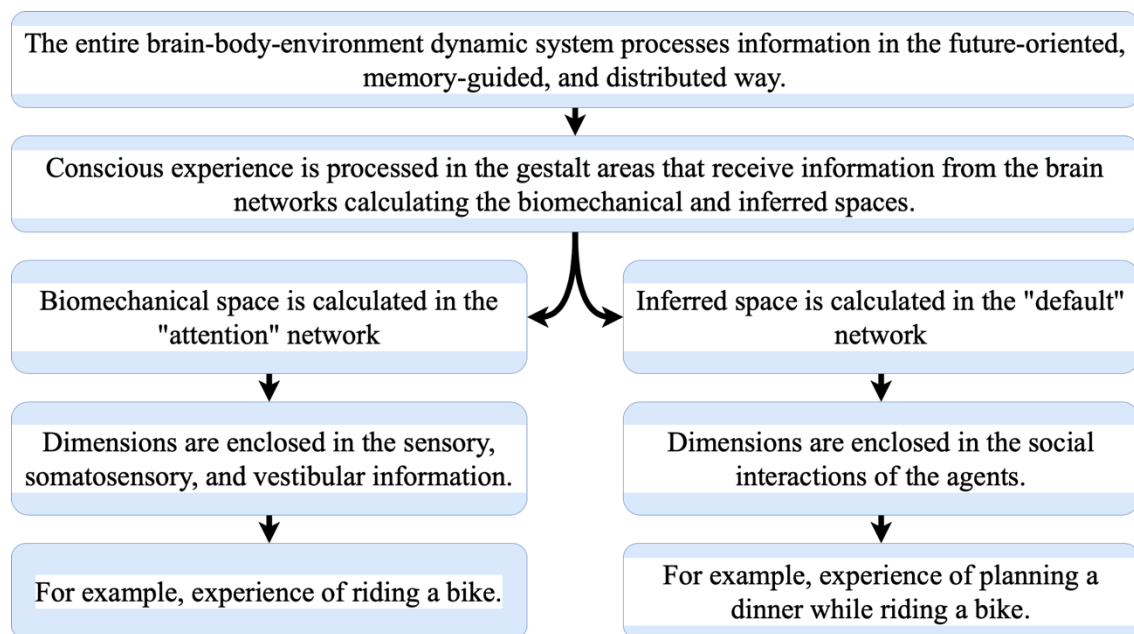
The **future-oriented information processing** is a consequence of the evolutionary processes. Adaptive systems anticipate their future to navigate it effectively (Bruineberg, Kiverstein, et al., 2018; A. Clark, 2013; Friston & Stephan, 2007). Navigating the surroundings involves navigating toward and away from specific futures, which is implemented by two evolutionary ancient motivational circuits: (I) reward-based and (II) misery-avoidant, processed by the nucleus accumbens and the amygdala, respectively (Loonen & Ivanova, 2015). Orientation toward the future is fundamental, given that surprise may imply receiving somatosensory information that will result in an organism's death.



The **memory-guided information processing** is a consequence of orientation toward the future. To construct accurate predictions, the system must store information about the already encountered statistical regularities. Memory is organized hierarchically, which is reflected in numerous frameworks such as Bayesian inference (Friston & Stephan, 2007), hierarchical processing of affordances in the Feedback Control Theory (Pezzulo & Cisek, 2016), a capacity to hold an optimal grip in the field of affordances in the Skilled Intentionality Framework (Rietveld et al., 2018), also as Cognitive Control given the broad context (Badre, 2008) and executive control over selecting actions and thoughts relative to internal intentional states (Koechlin & Summerfield, 2007). Complex hierarchical actions are understood as supervised movement sequences (Desrochers et al., 2016), which require cognitive control over action selection (Badre et al., 2009). In a branch of study focusing on the hippocampus, such actions are named “cognitive skills” (Cohen & Squire, 1980) and are associated with planning and counterfactual thinking (Squire, 2009b). The hierarchical organization of actions is also articulated in psychology and economy as a capacity for delayed gratification (Kahneman, 2013). Thus, this type of memory organization is widely recognized across the literature.

The three principles lead to the developing of a coherent and interdisciplinary conceptual framework of information processing in action. Fundamentally, organisms are systems processing information according to the above principles. The experience of the surroundings originates in the gestalt areas that receive information from the biomechanical space computed in the “attention” network and inferred space calculated in the “default” network decoupled from the incoming flow. The networks shape each other’s ontogenetic development (M. Chen et al., 2022) and are varyingly active depending on task demands (Dixon et al., 2018). Thus, the spaces computed in the networks significantly influence each other. Inference of the space of hidden causes behind the experience changes the meaning of the incoming information (Babayan et al., 2018; M. Chen et al., 2022; Nour et al., 2018), which is captured as a subjectivity of the experienced meaning (Ross & Ward, 1996). Given the complexity of the mutual interactions of the networks computing the spaces, this work simplifies the biomechanical inferred spaces entering the gestalt areas as the experience of the surroundings (rich landscape of affordances). The information processing the both spaces is fundamentally future-oriented, and thus also hierarchical, as the hierarchical organization of the predictions is more efficient.

The entirety of the conscious experience is representational as it originates from the processed information reaching the gestalt areas. The conscious experience for action is an experience of the surroundings that is computed from the biomechanical and inferred spaces entering the gestalt areas (**Figure 6**). The biomechanical space is calculated with the “attention” network (Ptak et al., 2017; Uddin et al., 2019). The inferred space is computed with the “default” network, decoupled from inputs (C. Murphy et al., 2018) and processing social information (Buckner & DiNicola, 2019; Li et al., 2014; Uddin et al., 2019; Yeshurun et al., 2021). During the ontogenetic development, the networks train each other in multiple ways (M. Chen et al., 2022; Dixon et al., 2017; Gao et al., 2013; Spreng et al., 2016). The activity of the two networks is controlled with a third “control” network, which includes some of the gestalt areas and mediates executive functions (Dixon et al., 2018; Uddin et al., 2019). The computations in the networks parallel the information processing in the two memory systems.



**Figure 6. The conceptual framework of information processing in action.** The conscious experience of the surroundings is computed from the biomechanical and inferred spaces. The former space is computed in the “attention” network, the latter in the “default” network. The dimensions of the biomechanical spaces consist of the sensory, somatosensory, and vestibular information, while the dimensions of the inferred spaces is abstract associations such as social interactions. The networks interact independently from the gestalt areas thus, their training during ontogeny remains to be investigated.

The conceptual framework developed in this work attempts to establish the interdisciplinary dialogue between cognitive sciences. While scholars trained in narrow

specializations investigate the structure of problem spaces, various kinds of attention and memory systems, semantics and syntax, and neurotransmitter systems; only some attempt to relate these research fields. As a result, the deep philosophical questions about the nature of existence, reality, or consciousness still need to be answered (Vervaeke et al., 2017). These questions arguably can only be asked understandably with coherent interdisciplinary terms. This is vital since existence, reality, or consciousness transcend things investigated in specific disciplines. Yet, no definition of existence, reality, or consciousness would enclose all these perspectives. This interdisciplinarity is needed to understand our place in the world and ourselves in terms of biology and psychology. The first step toward this understanding is developing a conceptual framework that would connect the disciplines in a genuinely interdisciplinary way. Once this understanding is achieved, more accurate questions concerning cognitive processes can be asked, potentially leading to a more in-depth understanding of human nature.

The search for interdisciplinarity in exploring what cognition is started its formal history at the first meeting of the Cognitive Science Society in 1979. At its dawn, the project aimed to establish a collaboration between scholars from various disciplines to understand how the mind emerges from information processing in the brain. The disciplines recognized in the society included **computer science**, which had been heavily influenced by cybernetics from the 1930s and '40s. Pioneers such as von Neumann, Minsky, and Turing contributed to developing the first computers. Today, cybernetics ideas are implemented in optimal control theory (Todorov, 2004) or predictive accounts of the brain (Friston, 2012). In **psychology**, flexible latent learning (Tolman, 1948) and language creativity (Chomsky, 1959) were contrasted with inflexible behaviorist accounts. Psychological research on memory began in 1952 with studies on the patient H.M. by Brenda Milner, which led to the discovery of two separate long-term memory systems known as declarative and procedural memory (Squire, 2009a). These observations inspired the progress in **neuroscience**, which has been experiencing tremendous development since the discovery of the DNA structure in 1953. In **linguistics** and **anthropology**, scholars such as Sapir and Whorf recognized that language shapes thoughts (Wolff & Holmes, 2011) and that understanding a given ethnic group requires cross-cultural translation of a broader context (Buden et al., 2009). **Philosophy** makes one ask fundamental questions and provides tools for reasoning such as abductive cognition, reasoning from first principles, and ontological methods for categorizing terms

used in particular disciplines and identifying which tokens of observations shall be interpreted as similar enough to be classified into a specific category.

This work connects the ideas from various disciplines of cognitive sciences to develop a broad understanding of human mental processes. In the last century, physics described general relativity and quantum theories, chemistry classified atoms and substances, and biology discovered evolution. The author urges similar efforts in sciences investigating cognitive processes and profound questions about the mind, consciousness, and our place in the universe. This effort requires recruiting onboard scholars from numerous disciplines as our civilization develops at an unprecedented pace toward the unknown future. We ought to be able to formulate precisely the deep existential questions and launch an effort in search of the answers.

The need is existential. To identify the direction where the next generations will find themselves, we must classify the mechanisms that influence our decisions and actions on numerous levels of complexity, from gene expression to electrical and chemical communication to social interactions. These levels are connected because each of us embodies a simultaneous existence on all these levels, yet they still need to be comprehensively addressed in scientific writings.

Today's fragmented knowledge is hardly accessible, given the specificity of language. The sheer number of concepts used to explain cognitive phenomena is baffling. The same phenomenon is captured with different labels, and the same labels denote diverse mechanisms. Navigating through this equivocacy requires such training that the sense of understanding is lost along the way.

The need for understanding has been pursued by such people as Hume, Descartes, Nietzsche, Heidegger, Kant, Jung, Darwin, James, Turing, Piaget, and Gibson. Naturally, the progress in this direction is ongoing. Contemporary scholars such as Sapolsky, Letvin, Wolfram, Vervaeke, and Bach pursue these questions. Nevertheless, this work argues that more is needed. Thus, this need is addressed by bridging the perspectives in a search for a genuine understanding of existence.

The framework developed here tackles the mind-body problem by treating animals as systems processing information in a **distributed, future-oriented, and memory-guided** manner. Then, a subset of this information processing related to action acquisition and execution is reviewed. The conscious experience of surroundings for action is linked to the information processing in memory systems, large-scale brain networks, and neurotransmitters' modulation of this information processing. The

framework explains how one infers everyday beliefs as part of one's experience by relating the conscious experience to the activity of brain networks. The review of the brain networks explores the information exchange within and between the brain networks. The analysis of the phenomenological evidence links the experience to the brain's activity, finding a potential home for the mind.

## 1. The description of the biological body in the physical space

The biological body in the physical space is operationalized in this chapter according to biomechanical and neuroscientific evidence. The processed information is conveyed by the sensory, somatosensory, and vestibular receptors that an organism is equipped with – its Umwelt. These information-processing channels are investigated in biomechanics (Knudson, 2021) and are grounded in animal brain regions underlying computation of body schema, tool use, and peripersonal spaces (Làdavas, 2002; Lopez, 2015; Maravita & Iriki, 2004; Serino, 2019), including parietal, frontal, and subcortical areas. As a result, the observations of the biomechanics of living beings and the neurobiological information behind these overt behaviors comprehensively describe a biological body in the physical space.

## 1.1 Information processing by the biological body

A biological agent is described with three information processing channels: sensory, vestibular, and somatosensory (Mergner & Rosemeier, 1998; Nashner, 2014) (**Table 1**).

Modality	Dimensions	Experience
<b>Somatosensory channel</b>		
<b>Pain</b>	sharp cutting pain	sharp cutting pain
	dull burning pain	dull burning pain
	deep aching pain	deep aching pain
<b>Temperature</b>	warm/hot	warm/hot
	cool/cold	cool/cold
<b>Touch</b>	itch/tickle and crude touch	itch/tickle and crude touch
	discriminative touch	touch
		pressure
		flutter
<b>Proprioception</b>	Position: Static Forces	vibration
		muscle length
		muscle tension
	Movement: Dynamic Forces	joint pressure
		muscle length
		muscle tension
<b>Vestibular channel</b>		
<b>Spatial orientation</b>	linear motion	acceleration / deceleration
	angular motion	rotating head
	tilt	nodding head
<b>Balance</b>	vestibular-ocular reflex	keeping the gaze fixed despite body movements
	vestibulospinal reflex	keeping the mass' centre of the body balanced
<b>Sensory channel</b>		
<b>Chemical</b>	olfaction	smell
	gustation	taste
	trigeminal chemosensory system	detection of chemicals with smell
<b>Mechanical</b>	cochlea's structures' vibration	sound
<b>Electromagnetic</b>	electromagnetic wave	vision
<b>Electric</b>	electroreception	electric field
<b>Magnetic</b>	magnetoreception	magnetic field

**Table 1. Information describing the biological body in the physical space.** Organisms process information divided into three channels: somatosensory, vestibular, and sensory. The information processing in the somatosensory channel results in the experiences of specific states of the body. The information processing in the vestibular channel results in the experiences of the movement of the body and body parts. The information processing in the sensory channel results in the experience of the external world (adapted from (Dougherty, 2020)).

The **somatosensory** channel processes pain, pressure, temperature, vibration, and proprioception (Raju & Tadi, 2021). Physiological pathways for conveying the somatosensory input are robust and reach many brain networks (McGlone & Reilly,

2010; ten Donkelaar et al., 2020). Here, the somatosensory information is recognized as crucial for an organism's locomotion as it is a feedback signal (Frigon et al., 2021) processed initially in the primary somatosensory cortex (Raju & Tadi, 2021). This information is particularly relevant from the perspective of future-oriented information processing, as an animal acts based on the *predicted* somatosensory information because somatosensory surprise may imply death.

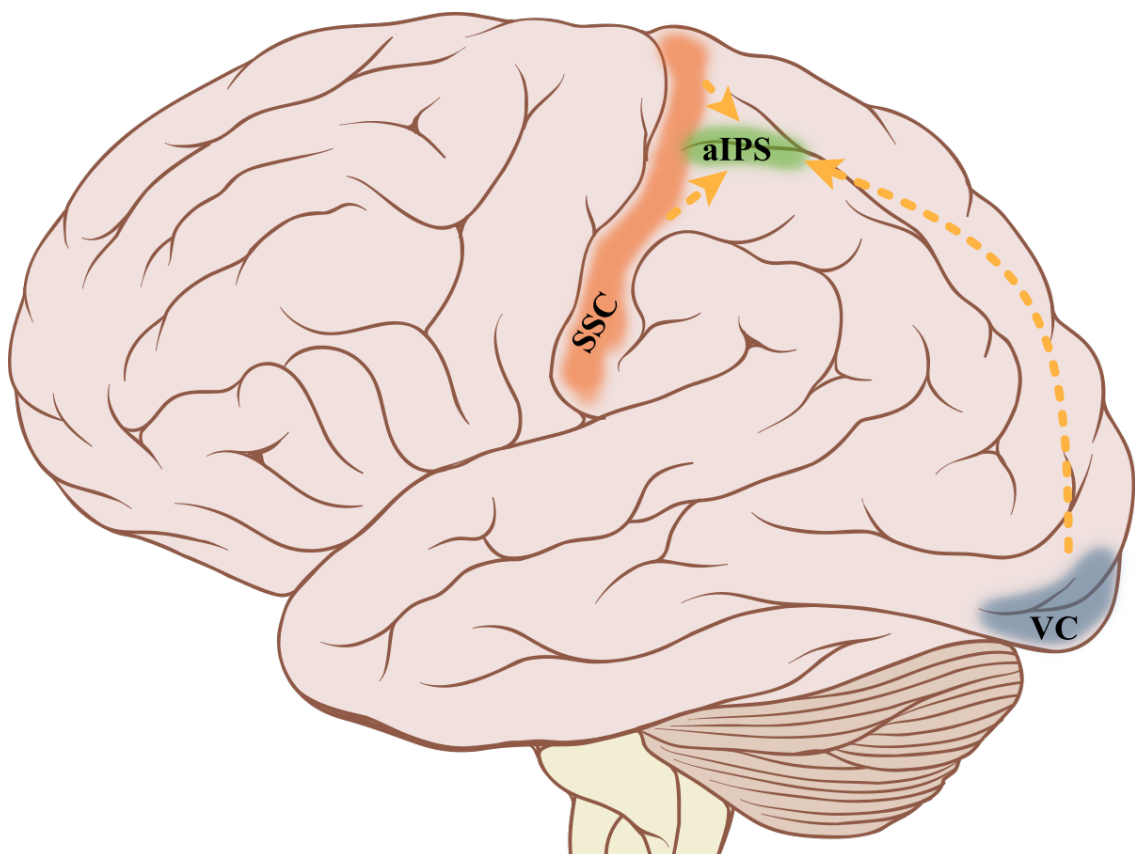
The **vestibular** input reaches multiple brain regions, including parietal and associative areas (Lopez, 2015) and the hippocampus (P. F. Smith et al., 2005; Stackman et al., 2002). The vestibular channel starts in the vestibular system located in the inner ear. It is crucial for maintaining balance, perspective, and equilibrium (e.g., which way is “up”) (Day & Fitzpatrick, 2005). The system senses gravity and acceleration/deceleration. It is responsible for the vestibular-ocular reflex (keeping the gaze fixed despite body movements) and the vestibulospinal reflex (maintaining body balance) (Kent et al., 2010). In general, the vestibular system tracks the tilt and rotation of the head and the body's horizontal and vertical acceleration, which follows information about the body's kinetics.

The **sensory** channel detects information from the physical world with specialized receptors that strongly depend on an organism's phylogeny. For example, chemical receptors are experienced as smell and taste, sensory mechanical receptors are experienced as sound and electric and magnetic receptors are found in non-human organisms. Primates rely primarily on the electromagnetic receptors tuned to the visible spectrum of the electromagnetic wave (Barton, 1998). This input is part of the scaffold for postural control, motion perception, and vestibular and somatosensory channels (Mergner & Rosemeier, 1998).



## 1.2 Processing information from the receptors

The claim that the three information channels fully describe the information processing performed by a biological body is supported by the architecture of information processing in the brain. For example, in primates, visual information diverges into two interconnected streams of information processing: dorsal and ventral (Milner, 2017). The dorsal visual stream conveys information about the location of objects and terminates in the parietal associative areas, where it is combined with somatosensory information from the rostrally located somatosensory cortex (Avillac et al., 2005, 2007; Iriki & Taoka, 2012) (**Figure 7**). The auditory and vestibular information also reaches this region of the brain (Day & Fitzpatrick, 2005; Lopez, 2015; Regenbogen et al., 2018).



**Figure 7. Parietal associative areas.** Intraparietal sulcus (green) combines somatosensory (orange), visual (blue), auditory (not shown), and vestibular (not shown) information into the multimodal computation of space around particular body parts (Lopez & Blanke, 2011; Serino, 2019), the space elongates with tools (Maravita & Iriki, 2004). The visual cortex is enclosed into one of the large-scale brain networks, including striatal and extrastriatal areas processing visual information (Uddin et al., 2019) from where visual streams originate (Milner, 2017).

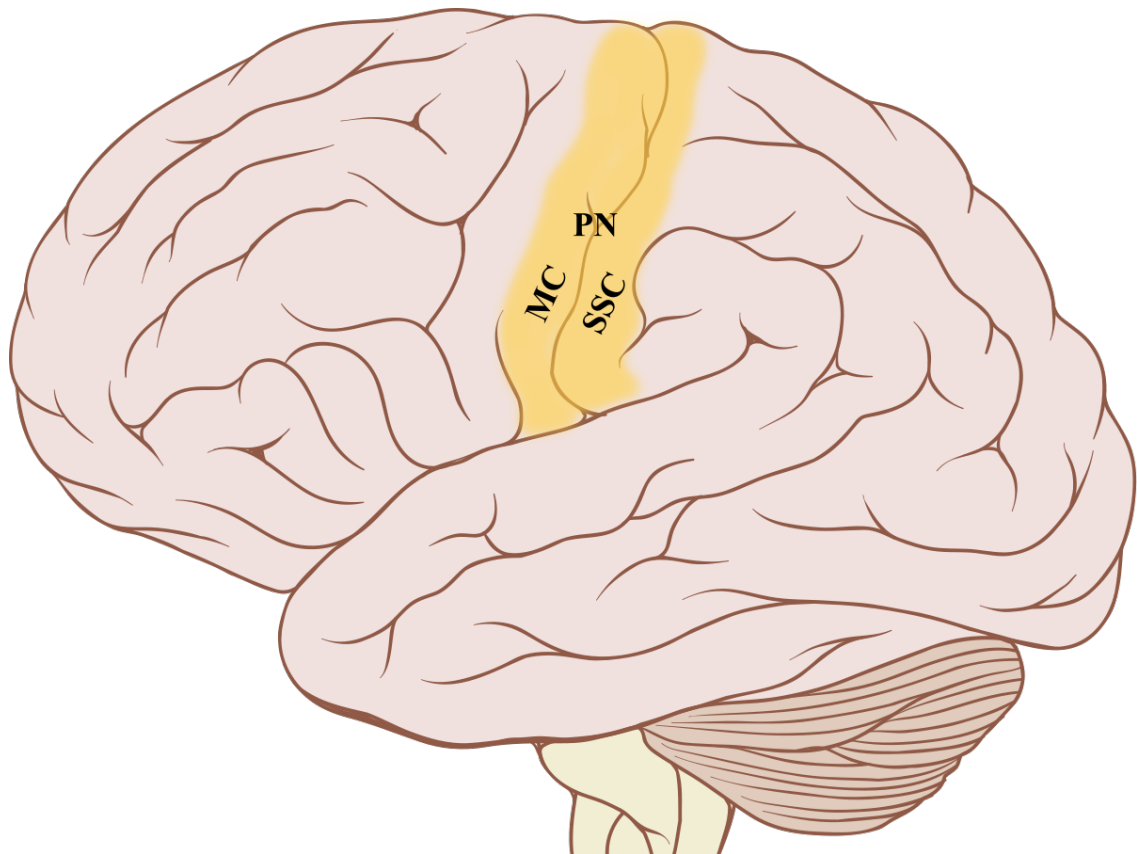
The information from the channels is jointly processed in the associative brain areas. The intraparietal sulcus combines somatosensory and visual streams at the level of single cells called bimodal cells (Maravita & Iriki, 2004). Some studies suggest that these cells should be called multimodal cells as they express sensitivity to auditory information (Duhamel et al., 1998; Guipponi et al., 2013). Thus, the associative brain areas process information about the body's position relative to the external world by combining sensory and somatosensory channels. Additional evidence suggests that associative regions of the parietal cortex receive input from the vestibular system (Lopez, 2015), hinting that the parietal associative area associates the entirety of the information about the biological body in physical space. Associative areas are found in other brain regions, such as the prefrontal regions (Lopez, 2015; Preuss & Wise, 2022). Given that the parietal and frontal areas are functionally coupled within the large-scale brain networks (Uddin et al., 2019), the associative areas are understood as computing the information about the biological body in the physical space by combining sensory, somatosensory, and vestibular inputs.

Research on the associative areas in the parietal cortex reveals that information processing of the space around the body is highly organized into distinct peripersonal spaces (Serino, 2019). These peri-spaces are attached to specific body parts, such as peri-arm and peri-hand (Graziano & Gross, 1993; Guipponi et al., 2013; Làdavas, 2002; Niu et al., 2021), and their activity is gradual and action-oriented (Bufacchi & Iannetti, 2018). In other words, peri-spaces are parts of the sensory (visual) experience of objects capable of generating somatosensory and vestibular feedback. These computations are subjective to the animal's mechanical properties (e.g., speed, acceleration, inertia) (Bufacchi & Iannetti, 2018; Galli et al., 2015). For example, modifying vestibular information by changes to animals' characteristics of potential vectors of movement (e.g., when driving a car or a wheelchair) changes the neuronal computation of the peri-spaces. This points out that modifying the capacity to move results in changes in the calculation of visual information. This is investigated in experiments on tool use in primates and humans.

Tools are modifications to an animal's biomechanical properties distributed on the spectrum between translating output forces smoothly (e.g., pushing, pulling, rotating) and abruptly (e.g., hitting). Experiments on macaque monkeys reveal multimodal cells sensitive to visual and tactile information (S. Gallagher, 1986; Maravita & Iriki, 2004). Touching the hand/arm and shining light close to the hand/arm elicit activity of the same region specific to the hand/arm. A skillful grip on a tool elongates the cells' visual receptive field with the tool's range (Aglioti et al., 1996; Berti & Frassinetti, 2000). Such

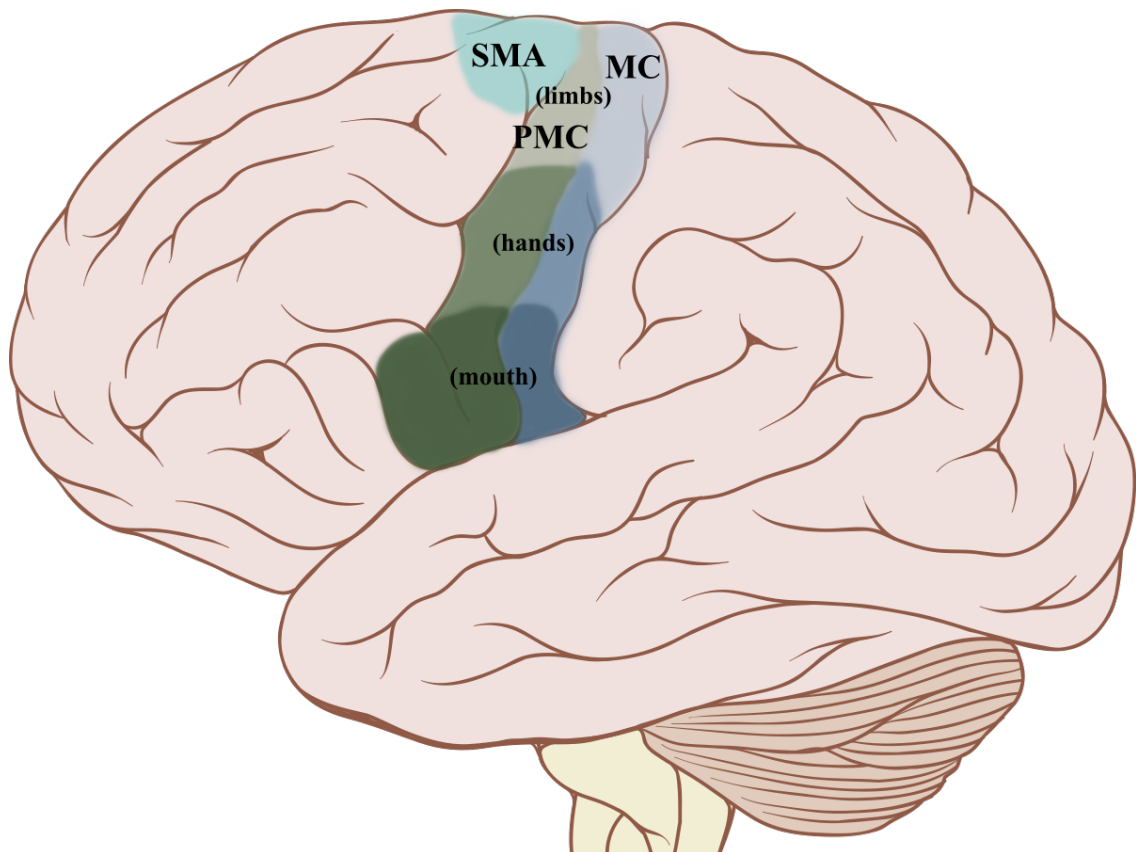
associative information computation is identified in numerous parts of the macaque brain: the putamen (Graziano & Gross, 1993), superior colliculus (Wallace et al., 1996), parietal (Duhamel et al., 1998; Graziano & Gross, 1993; Hyv rinen, 1981), and frontal cortices (Graziano & Gross, 1993; Graziano et al., 1999; Rizzolatti et al., 1981). These observations have been partially translated into research on humans (Berti & Frassinetti, 2000; Gentile et al., 2011; Guipponi et al., 2013; Guterstam et al., 2015). For example, changes in the peri-spaces have been identified in patients suffering from unilateral neglect and participants navigating with a wheelchair.

The associative processing of information also occurs at the level of large-scale brain networks (Uddin et al., 2019). One of the networks, the Pericentral Network (PN), is located on both sides of the central sulcus and combines information from motor and somatosensory cortices, as shown in **Figure 8**.



**Figure 8. The pericentral network.** One of the large-scale brain networks that jointly process motor information is the Pericentral Network (PN), enclosing the Motor Cortex (MC) and the somatosensory cortex (SSC) (Uddin et al., 2019). The information processing in the PN contributes to movement acquisition and execution and is discussed further in section 5.2.

The organization of the PN can be further divided into three sections specialized in processing information related to particular body parts: ventral (mouth), lateral (hands), and dorsomedial (feet) (Gordon et al., 2023; Graziano, 2016; Raju & Tadi, 2021) (**Figure 9**). The PN contributes to various motor behaviors, known as species-specific fixed motor patterns (Lorenz, 1981), movements of body parts (limbs, mouth) (Graziano, 2016), and stereotypic behaviors (Berridge et al., 2005; Reason, 1990).



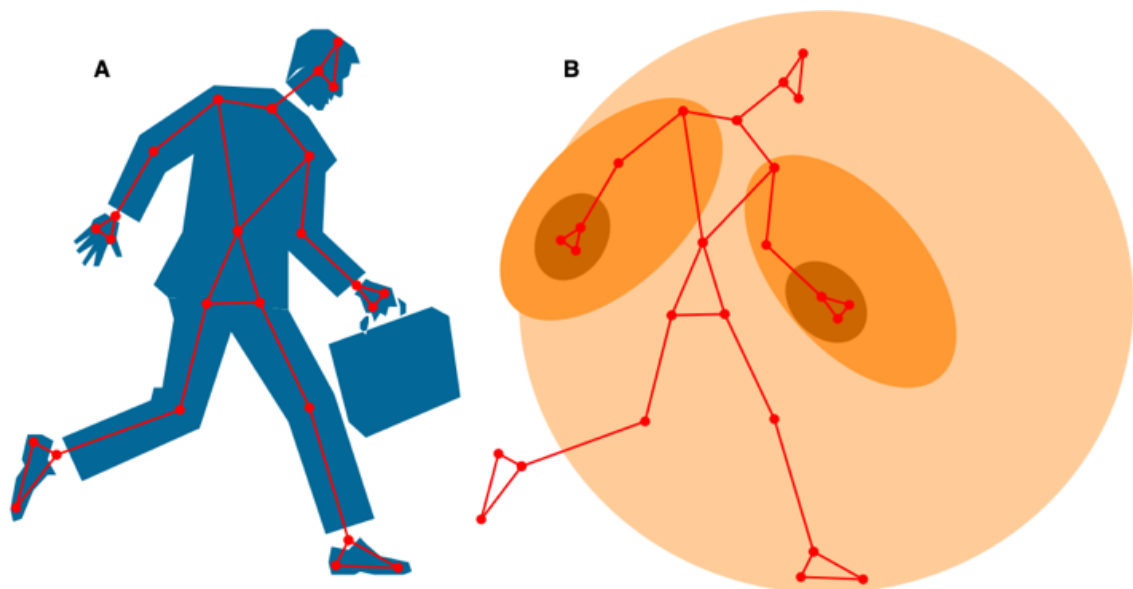
**Figure 9. Frontal motor areas.** The motor cortex (MC) and the premotor cortex (PMC) compute the movements of the mouth, hands, and limbs in the ventral-dorsal organization of information processing (Graziano, 2016). Such information processing organization is reflected in the architecture of the entirety of the PN (Gordon et al., 2023; Raju & Tadi, 2021). The literature points to an orthogonal division spanning the rostral-caudal axis of the motor areas: anteriorly located PMC computes multi-limb actions, and posteriorly located MC is preferentially active in single-limb movements (Graziano, 2016). Further, the PMC prepares activities related to external cues (Rizzolatti et al., 1996, 2002), whereas the supplementary motor area (SMA) extending toward the medial part of the brain calculates the preparation of the multi-limb actions linked to internal prompts (Nachev et al., 2008).

It should be noted that the precision of action increases ventrally as mouth and pharynx movements produce high-resolution articulatory gestures (actions making sound), which have been identified in humans' ventral precentral gyrus with a direct

electrophysiological recording of the brain of epileptic patients (Mugler et al., 2018). Movement of the pharynx is thus recognized as mediated by ventral sections of the motor (Graziano, 2016) and somatosensory (Raju & Tadi, 2021) cortices. Accordingly, communicative sounds such as deontic actions (Constant et al., 2019) are interpreted here as actions that, in principle, may rely on the information processing within the PN.

### 1.3 Biomechanics of the biological body

Biological bodies existing in the physical space are investigated in a branch of physics called biomechanics (Knudson, 2021). Forces acting on a body (which causes, inhibits, facilitates, or modifies movement) are studied as kinetics. In contrast, spatiotemporal characteristics of motion in the Cartesian coordinate system without regard to the causative forces are studied as kinematics (Jensen, 2005; McLester & St. Pierre, 2008; Serway & Jewett, 2018). In biomechanics, the body is modeled as a free-body diagram that captures a system of interest (e.g., an arm or a body) and the degrees of freedom that this system has (e.g., what movements are possible) (Rodrigo & Ambrósio, 2011) (Figure 10).



**Figure 10. A simplified biomechanical model of a body.** a) The red graph (nodes and edges) is a biomechanical model of a biological system capturing the position of the joints; forces acting on the body have not been shown (Knudson, 2021). b) Orange ellipses roughly denote visual space around the body computed in the brain in a specific way known as peripersonal space (Serino, 2019), which is extendable with tools computed in primates' intraparietal sulcus (Maravita & Iriki, 2004).

Biomechanics is applied in studies of motor control (Latash & Zatsiorsky, 2016; Winter, 2009), in particular in the field of motor development (J. E. Clark & Whittall, 2021; Jensen, 2005; Jensen & Korff, 2005) and motor learning (Di Domenico, 2020; Keogh & Hume, 2012; Raiola, 2014). Biomechanical data are collected with high-speed sensitive cameras capturing the position of the joints and degrees of freedom of the biomechanical system of interest. Some studies apply biomechanics to analyzing

sensorimotor systems of the brain (Lin et al., 2019; Schouenborg, 2004). However, most studies do not recognize biomechanical methodology in research on acquiring sensorimotor skills (Christensen et al., 2019; Kee, 2019; Nackaerts et al., 2019; Popp et al., 2018; Yin & Knowlton, 2006; Yokoi et al., 2018) or procedural learning (Henke, 2010; Mason & Just, 2020; J. N. Williams, 2020)<sup>1</sup>.

It is claimed here that the biomechanical methodology is well suited to operationalizing skills researched in psychology, where skills are divided into “sensorimotor” and “cognitive” skills (Ackerman & Cianciolo, 2000; Cohen & Squire, 1980; Graybiel & Grafton, 2015; Hikosaka et al., 2002; Raiola, 2014). The field uses confusing terminology, as the acquisition of a sensorimotor procedure is described in three phases: cognitive, associative, and autonomous (Fitts & Posner, 1967; Kee, 2019). The cognitive phase of learning a sensorimotor skill often goes beyond procedural memory and engages episodic and working memory (Ackerman & Cianciolo, 2000). Here, skills refer only to the final stage, where a sensorimotor procedure is fully automated.

Given the operationalization of the biological body as a system processing sensory, somatosensory, and vestibular channels of information, skill learning is understood as encoding information flow within these channels into long-term memory (see Section 4.2). Skill acquisition investigated in biomechanics acknowledges a spectrum between “open skills,” executed in unpredictable situations (like diving to block a penalty, maneuvering a ball in a team sport, or surfing), and “closed skills” performed in relatively stable situations (such as a gymnastics routine, running, or serving a ball) (Gu et al., 2019). This division reflects the cognitive and associative phases of skill acquisition that are subsumed with the autonomous phase when the skill is finally acquired (Ackerman & Cianciolo, 2000; Kee, 2019). In other words, with training, circumstances become encoded, and a skill gradually closes. Closing a skill means performing it without encountering surprises, i.e., a transition is accurately retrieved. Thus, here, only the “closed skills” meet the definition for skills, as “open skills” encounter surprisal and are not yet automated, thus relying on the memory system

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<sup>1</sup> It is hypothesised that applying the biomechanical methodology to psychological and neuroscientific research on skills is essential in understanding skills acquisition and maintenance. Further, the biomechanical model capturing agents’ actions and forces influencing these provide mathematical operationalization, which can be compared with underlying brain activity in the search for regularities. Such an approach seems to be particularly relevant for monitoring movement and brain abnormalities in the early stages of neurodegenerative diseases such as Parkinson’s Disease.

beyond the one controlling the flow of sensory, somatosensory, and vestibular information.

The division for perceptual-motor and cognitive skills rely on the preservation (or impairment) of the ability to learn and perform skill by patients with degeneration involving the hippocampus (Gabrieli, 1998). For example, an amnesic patient known as H.M. encodes perceptual-motor tasks such as the pursuit rotor task or mirror tracing task, but his capacity to solve planning and problem-solving (e.g., tower) tasks was severely impaired (Saint-Cyr et al., 1988; Y. Xu & Corkin, 2001). Nonetheless, in certain circumstances, amnesic patients can perform well in tasks from the cognitive category (Knowlton et al., 1992). Still, relative to the control group, they show deficits (Butters et al., 1985), presumably showing an alternative strategy for skill acquisition (Ullman, 2004). The above studies indicate that performing a skill understood as changes in the flow of sensory, somatosensory, and vestibular information can result from heterogeneous information processing. This work distinguishes a memory system coupled with the ongoing flow of information and one dissociated from this flow (see Sections 3.2, 5.1).

Computationally, skill learning relies on adjusting the information flow from exploration to exploitation. This dilemma is central to any self-adaptive system and has no trivial solution (Berger-Tal et al., 2014; Wilson et al., 2021). Exploitative actions generate anticipated feedback; exploration is a heterogeneous term roughly defined in the field into broad classes of “random” and “directed” exploration (Gershman, 2019; Gigerenzer & Gaissmaier, 2011; Wilson et al., 2021; Wilson, Geana, et al., 2014). The volatility of the environment (Findling et al., 2019), time horizon (Berger-Tal et al., 2014), and age (Dubois et al., 2022) influence the balance between exploration and exploitation. Directed exploration is thus akin to an educated guess reflecting the hypothesis of a specific transition in time. An animal learns the information flow in the sensory, somatosensory, and vestibular channels to the extent that the flow is sufficiently anticipated and hence exploited as a skill.

According to optimal control theory, it is understood that skills are reliably performed despite the variability in the information flow (Todorov, 2004). This means recalling the skills is never *precisely* the same, as the muscle movements express a degree of variability at low resolution. In the free energy literature, this variability of information is captured within the redundant subspaces (A. Clark, 2015, p. 119; Todorov & Jordan, 2002), a notion developed from “the minimal intervention principle” proposed by



Todorov and Jordan (2002). It allows for variations at lower layers of information processing relative to the layer at which the outcome is anticipated, encapsulating the range of expected variability of the transition. An animal acquires a skill when its execution repetitively does not generate surprise. In other words, feedback fits into redundant subspace, and transition in time is successfully retrieved from the memory.

## 1.4 Summary

The biological body in the physical space is described as a system processing sensory, somatosensory, and vestibular information. Associative brain areas process these inputs, including parietal and frontal cortices and the pericentral network. These brain regions underpin computations of the peri-spaces around specific body parts processed as body extensions into the physical space. Tool use further extends the visual receptive fields of the peri-spaces. This converging evidence justifies the operationalization of biological bodies as processing sensory, somatosensory, and vestibular information.

The biological body observed from the outside is investigated in the branch of physics called biomechanics. In biomechanical analysis, bodily systems of interest are captured with fast-motion-sensitive cameras and analyzed with sophisticated software. This approach allows for the rigorous biomechanical investigation of body movements that can be fruitfully applied to psychological research.

## 2. Consciously experienced surroundings of multiple potential futures.

The operationalization of animals as information processing systems largely ignores the animal's phenomenological experience. The biomechanical analysis and the focus on sensory, somatosensory, and vestibular information processing in the brain emphasize the observed movements, such as skills. However, these observations are often tied to a specific phenomenological experience. Animals do not experience the flow of information processing per se; animals experience surroundings that are progressively more complex along the phylogenetic and ontogenetic development. The richness of phenomenological experience includes a broad spectrum of qualia, such as redness, emotions, or meaning. This work is concerned with the action-oriented qualia that are called affordances.

The hierarchical organization of affordances toward the potential futures originates from the principle of future orientation in information processing, which also applies to the information processing that underpins the experience of qualia. Originally, affordances were meant to capture relations between the configuration of joints, height, strength, or mass of an animal and the physical properties of its surroundings (Chemero, 2009; Gibson, 2014; Richardson et al., 2008). For example, a leaf affords support for an ant, a rock affords sitting for a human of a given height, and a river affords locomotion for a fish. However, when the term gained popularity, it was adopted to multiple novel domains and has obtained alternative meanings (Bruineberg & Rietveld, 2014; Cruz et al., 2018; Djebbara et al., 2020; Eismann et al., 2021; Pezzulo & Cisek, 2016; van Dijk, 2021). Contemporarily, affordances are understood as relations between an organism's capacities to act and the features of its surroundings that change in time (Chemero, 2001, 2003, 2009).

In general, affordances denote the pathways toward potential futures that can be reached with specific information flows in the sensory, somatosensory, and vestibular channels. The evolution put pressure on optimizing the accuracy of the anticipated futures, thus driving the need for the models of potential futures. In humans, the phenomenological experience of action-oriented qualia encloses the rich landscape of affordances named surroundings.

## 2.1 Affordances toward the potential futures

In biological and psychological sciences, the concept of an organism's living space varies from that in physics. Ecological psychology refers to it as an environment (Gibson, 2014), while evolutionary biology calls it a niche (Lewontin, 2000). Both disciplines agree that animals live in subjective surroundings. In ecological psychology, the environment denotes direct perceptual information that an animal can act upon; in evolutionary biology, the niche encapsulates how an organism lives. Ecological psychology understands animals as following the possibilities for action known as affordances (Gibson, 2014; Richardson et al., 2008). Affordances have been originally operationalized in ecological psychology as ever-changing features determined by the unique temporal-spatial location of the perceiver to an object (Gibson, 2014). Essentially, an organism is inseparable from its environment-niche, i.e., environment and niche always surround an organism and provide it with affordances.

The central figure in ecological psychology was J.J. Gibson, who introduced affordances, denoting the direct experience of opportunities for actions (Gibson, 1950, 2014). Gibson claimed that an organism's environment differs from the objective physical world. In his own words:

*If a terrestrial surface is nearly horizontal (instead of slanted), nearly flat (instead of convex or concave), and sufficiently extended (relative to the size of the animal) and if its substance is rigid (relative to the weight of the animal), then the surface affords support. (...) Note that the four properties listed—horizontal, flat, extended, and rigid— would be physical properties of a surface if they were measured with the scales and standard units used in physics. As an affordance of support for a species of animal, however, they have to be measured relative to the animal. They are unique for that animal. They are not just abstract physical properties. They have unity relative to the posture and behavior of the animal being considered. So an affordance cannot be measured as we measure in physics. (Gibson, 2014, pp. 119–120).*

Gibson's theory of affordances is grounded in the idea that the environment offers animals opportunities for actions unique to that specific animal. These opportunities are based on the animal's physiological characteristics, such as joint configuration and mass.

This intuition is grounded in the living space (umwelt), postulated by von Uexküll (Fultot & Turvey, 2019). In general, ecological psychology endorses the subjectivity of the relationships between biology and physics.

Chemero (2001) elaborated on the understanding of affordances, further supporting the notion that they should be viewed in a relative context. This was in response to frameworks that treated affordances as static properties of the world (Heft, 2001; Michaels, 2000; Reed, 1996). Chemero proposed the Affordances 2.0 theory, where the distribution between the organism's abilities to perceive and act and the features of its environment is understood as dynamic relations:

*To formulate Affordances 2.0, start with Affordances 1.1, according to which affordances are relations between abilities to perceive and act and features of the environment. Then consider the interaction over time between an animal's sensorimotor abilities, that is, its embodied capacities for perception and action, and its niche, that is, the set of affordances available to it. (Chemero, 2001, p. 111)*

Affordances 2.0 point to reciprocity in the system and emphasize that distributed information processing occurs in a temporal context. Following affordances involves transitioning toward specific potential futures that make subsequent affordances available. The understanding of affordances as dynamic, reciprocal relations within the distributed information-processing system is adopted here. As evolutionary biologists (Longo et al., 2012; Longo & Montévil, 2014) and philosophers (Bertolotti & Magnani, 2017) noted, the concept of "affordances" has become popular in cognitive sciences. They argue that affordances no longer refer solely to physical properties and suggest distinguishing between "biological enablements" and "psycho-cognitive affordances." For example, Bertolotti and Magnani refer to the New Caledonian crow, which can learn toolmaking through mechanical manipulation or social observation (Weir & Kacelnik, 2006). These studies emphasize the need for a more precise understanding of affordances because it became an umbrella term denoting all possibilities for action irrespective of the distribution type being acted upon. Nevertheless, most scholars use the notion of affordances broadly to indicate the rich landscape of invitations for action, and such convention is maintained in this work.

Taken together, affordances are understood as opportunities toward potential futures that a specific animal can reach. Affordances are action-oriented qualia; thus, they are subjective as the entirety of the phenomenological experience. The closeness to sensory, somatosensory, and vestibular inputs that can be experienced fully depends on the animal's phylogeny and ontogeny. Affordances thus reflect both (I) information processing performed close to the inputs and (II) advanced information processing decoupled from the inputs. For example, one can experience and act toward a future moment in dynamic team sports such as football or a future decoupled from inputs such as Moon colony. Both kinds of experience involve affordances with varying correlations with the ongoing flow of incoming information.

## 2.2 Surroundings denote environment and niche combined

Every animal is an information processing system with its own unique experience. This unique perspective on the world includes physical objects and social agents, as well as personal past and predictions for the future. This is especially true for complex information processing systems such as humans, as there is no clear boundary between the interior and exterior of the human. Clark and Chalmers (1998) realized that the animal extends with artifacts to augment information processing, pointing out that the brain is an interconnected network. Countless publications stress that animals are embodied, extended with artifacts and tools, enactively acting/interacting, and embedded with contexts such as one's history and plans for the future. Some accounts suggest that the brain is, in fact, 6e – also emotional and exapted (the latter being neuronal reuse/recycle). Similar ideas are also expressed in ecological-enactive writings where an animal is understood as a brain-body-environment dynamic system (Beer, 2008). Here, an animal is understood as an information processing system distributed onto objects, agents, and time. This distribution of the information processing system is consciously experienced as the landscape of hierarchically organized affordances that are called here the **surroundings**.

Affordances are action-oriented qualia that point to potential futures. The landscape of probable futures needs to be hierarchical, as imposing the hierarchical structure increases the accuracy of the predictions. The set of affordances accessible to an organism is called either an environment (Gibson, 2014) or a “niche” (Chemero, 2009). The understanding of the environment and the niche in the relevant literature overlap. Given that, the environment and the niche are combined into an umbrella term of surroundings that encloses the entirety of the future-oriented qualia experienced by a specific animal.

The niche is a term used in evolutionary biology that refers to *how* animal species live (Chase & Leibold, 2003; Odling-Smee et al., 2003; Pocheville, 2015). Ideally, a species would thrive in optimal conditions, but adaptation to sub-optimal circumstances is driven by evolutionary pressure and random factors. Hutchinson (1957) coined the term “realized niche” to describe this sub-optimal, inhabited niche. This understanding of the niche considers factors such as competition or scarcity of resources; thus, it is subjective to the specific species in specific conditions (Odling-Smee et al., 2013).

The term niche is widely used by cognitive scientists who applied it to “psycho-cognitive” circumstances (Bruineberg, Kiverstein, et al., 2018; A. Clark, 2006; Friston, 2011; Tooby & DeVore, 1987; Werner, 2021). Recall that the same observation has been made about the “biological enablements” and “psycho-cognitive affordances” (Bertolotti & Magnani, 2017; Longo et al., 2012; Longo & Montévil, 2014) (see Section 2.1). The mentioned authors suggested that enablements describe sensory, somatosensory, and vestibular information flows, whereas affordances denote the experience of social information processing. Nonetheless, when scholars across disciplines refer to biological and cognitive niches, they uniformly refer to “affordances” connecting the organism with its niche (Bruineberg, Kiverstein, et al., 2018; Iriki & Taoka, 2012; Pinker, 2013). If one accepts the philosophical argument, the biological niche is filled with enablements, and the cognitive niche is filled with affordances. However, here, the niche is operationalized in terms of the familiar affordances regardless of their distance from the inputs. For example, one can reliably imagine a memory palace dissociated from the incoming information (Mecacci, 2013), experienced without prediction errors, and thus, it constitutes a niche.

Since the niche denotes how an animal lives, it encapsulates an experience of affordances toward the potential futures that return the anticipated feedback. Following affordances involve changing the flows in sensory, somatosensory, and vestibular information that may predict the future accurately or may encounter prediction errors. Some affordances are “familiar” and can be reliably achieved, whereas others are “novel” and reaching them requires training. This distribution is the tradeoff between exploring the unknown and exploiting known affordances (see: Section 1.3).

In evolutionary biology, the term “niche construction” captures the mechanism of initial exploration and subsequent exploitation of the information in the surroundings. Animals create niches by altering their environment (perturbation) or changing the environment altogether (relocation). Niche construction is a process that works alongside natural selection, according to Odling-Smee et al. (2013). It involves animals expressing their genes not just through their physical characteristics but also through their actions, such as building beaver dams (Dawkins, 1982). By constructing their environment in a way that benefits their survival and the survival of their offspring, animals gradually develop their niches (Heras-Escribano & De Pinedo-García, 2018; Laland et al., 2015; Odling-Smee et al., 2013). Thus, niche construction is understood here as the initial



exploration of available affordances that, after repetitively acted upon, become the exploitative way of living for a given animal.

The process of niche construction captures a mechanism of initial encoding and subsequent retrieval of information stored in the agent's memory, which also applies to the organism's ontogeny. For example, primates from different tribes construct nests in specific ways (Boesch & Boesch, 1990; Hicks et al., 2019). In the case of humans, a variety of factors (including language, cultural, and social) play a significant role in shaping one's actions and worldview (A. Clark, 2006; A. Clark & Chalmers, 1998; Norman, 2013; Saarinen & Krueger, 2022; Taylor et al., 2011; Varela et al., 2017). In extreme circumstances, feral children of *H. sapiens* do not learn the niches that involve social interactions, and individuals with Savant's Syndrome learn extraordinarily detailed sensory niches. For *H. Sapiens*, ontogenetic development is a life-long process of developing knowledge structures (Piaget, 1970).

Complementary, scholars researching ecological-enactive information processing pointed out the distinction between available and relevant affordances (Bruineberg et al., 2019; Bruineberg, Kiverstein, et al., 2018; Rietveld et al., 2018). The field of "relevant affordances" has been conceptualized as "the field of solicitations" (Bruineberg et al., 2019; Rietveld et al., 2018). Solicitations refer to possibilities for action that stand out as essential to maintaining allostasis. The niche is a frequent experience of specific affordances that result in a particular way of living. Thus, these affordances are relevant for maintaining the distributed information processing system. When the familiar affordances are no longer experienced, the distribution of the system gradually shifts.

Similarly, in design literature, it has been noticed that a smartphone screen "invites" actions on its whole surface. However, only specific locations signify relevant activities (Norman, 2013). These observations point out that the affordances are experienced with varying frequency. Niche denotes exploitative affordances that are frequently experienced; environment denotes explorative affordances that are encountered less often.

The idea that the landscape of potential futures involves futures that have been visited in the past and the novel futures that are only hypothesized exemplifies a fundamental computational dilemma that any adaptive system faces. Namely, future surroundings are volatile, uncertain, complex, and ambiguous; thus, navigating them is

tied to uncertainty. An animal is unsure about future feedback; therefore, it faces the dilemma of exploring the unknown environment or exploiting the familiar niche.

### 2.3 Exploration-exploitation spectrum of affordances

Balancing between exploring new possibilities and exploiting the known ones is investigated in computational neuroscience (Dolan & Dayan, 2013; Sutton & Barto, 2018), and it has no trivial solution. The affordances are differentiated by appealing to the exploration-exploitation spectrum, i.e., to their familiarity. Exploration means trying something new with unknown consequences. If it works out well, it can be repeated in anticipation of obtaining the same results, at which point the repeated action becomes exploitative. The niche comprises the exploitable affordances defining an animal's way of life, whereas the environment encompasses explorable affordances.

The spectrum is investigated in experimental research on humans, where many factors influence whether one explores or exploits one's surroundings, including the available time horizon (Berger-Tal et al., 2014), age (Dubois et al., 2022), or volatility of the environment (Findling et al., 2019). Exploration can be done randomly or with a specific goal in mind (Wilson, Geana, et al., 2014), and it can involve using heuristics to guide the process (Dubois et al., 2021, 2022; Gigerenzer & Gaissmaier, 2011)<sup>2</sup>. For example, experimental data show that saccades are directed to the most informative places and that their nature shift from reactive to proactive along a transition from uncertain to predictable circumstances (Donnarumma et al., 2017). The familiarity of the incoming information determines whether the incoming flow of sensory, somatosensory, and vestibular information is surprising.

An environment and a niche are *always* understood as relative to the ontogeny and phylogeny of an animal experiencing it. The environment includes all experienced affordances; the niche includes known affordances. The spectrum between explorative and exploitative affordances underpins the range between the environment and niche. An animal is thus understood as experiencing explorative affordances (comprising the environment) and exploitative affordances (constituting the niche).

The shift from exploration to exploitation is reflected in research on habit formation. In psychology, habits refer to automatic behaviors triggered by cues associated with past performances (Neal et al., 2006). Habits are learned tendencies to repeat previous actions in a given circumstance (Wood & Neal, 2007). They are often considered a part of a routine, such as tying shoes after putting them on (Graybiel & Grafton, 2015). Habits can be broken down into smaller chunks, but these chunks tend

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<sup>2</sup> Directed and random exploration can be referred to as convergent and divergent creative thinking.

to group (Dezfouli et al., 2014; Dezfouli & Balleine, 2012). Habits are typically initiated by a cue eliciting the remaining steps without engaging in decision-making. This implies that habits are conceptually equal to exploitative affordances underpinning an animal's niche. Evolutionary speaking, an animal repetitively following exploitative affordances in its niche is, from a psychological perspective, engaging in habitual behaviors.

Actions are investigated not only as “habits”, but also as “skills” (Ackerman & Cianciolo, 2000; Cohen & Squire, 1980; Graybiel & Grafton, 2015; Hikosaka et al., 2002; Raiola, 2014). Biomechanically, skills are enclosed in the spectrum between open and closed skills (see: Section 1.3). Psychological literature differentiates three phases of skill learning: cognitive, associative, and autonomous (Fitts & Posner, 1967; Kee, 2019). The cognitive phase involves episodic and working memory (Ackerman & Cianciolo, 2000). Note that the initial learning of a skill and its subsequent automatization reflects a gradual progression from exploration toward exploitation of affordances.

Skill and habit learning is understood here as involving two stages: (I) learning how to move the body and (II) learning the feedback to these movements. More precisely, (I) the initial stages of learning are understood as learning the information flow to balance the body's movements and find the *sufficient* transition toward a specific potential future. Once adequate move is discovered, (II) the subsequent stages of learning shift the information processing toward focusing on increasing the *accuracy* of the transition in time. Once a sufficient conversion in time is identified, its execution leads to an increase in accuracy, which reflects the development of the redundant subspace described in optimal control literature (Todorov, 2004; Todorov & Jordan, 2002). A sensorimotor procedure gradually becomes a learned exploitative affordance underpinning an animal's niche.

The process of learning action is investigated in neuroscience. Researchers have studied habits and instrumental activities under various names for nearly a century. Tolman's (1948) cognitive maps and Thorndike's (1898) stimulus-response account were initially compared. Later generations of research focused on goal-oriented and habitual actions in rodents (Balleine, 2005; Balleine & Dickinson, 1998; Killcross, 2003) and humans (Tricomi et al., 2009; Valentin et al., 2007).

The contrast between habits and goal-oriented actions can be misleading, implying a criterion related to a specific outcome. The neuroscientific definition of goal-oriented actions is that a goal-oriented action (I) reflects knowledge of the relationship between an action (or sequence of actions) and its consequences, which is known as

response outcome control, and that (II) the outcome should be motivationally relevant or desirable at the moment of choice. „*Crudely, subjects choose actions because they think that those actions lead to outcomes that they presently desire.*” (Dolan & Dayan, 2013, p. 314). In contrast, habitual actions are based on repeating past actions that have led to positive outcomes but may not necessarily be linked to the desired result at the present moment. The above criteria were initially developed in animal research and directly adapted to human research (Dickinson, 1994) without recognizing the complexity of the human phenomenological experience (Bratman, 1991; Mele, 1992; Pacherie, 2008; Searle, 1983). This complexity of intentional states in *H.Sapiens* makes direct translation of *desirable conditions* from the rodent literature inappropriate. Humans express contradictory desires and complex sets of intentions. Further, humans (and other cognitively advanced organisms) can postpone the rewards, desire things they do not intend, and intend to do something they do not want. Thus, the difference between goal-oriented and habitual instrumental actions concerns the automation along the exploration-exploitation spectrum, not the post hoc judgment of the feedback from following the affordance.

For example, a neuroscientific test for habitual behavior relies on the initial automatization of action in a specific environment and then changing the structure of this environment. Habit is diagnosed when an animal performs a trained action despite the satiation or absence of the reward (Dolan & Dayan, 2013). Initially, the behavior is goal-oriented but can become habitual in the right circumstances (Poldrack & Packard, 2003). The degree of habitual behavior is measured by observing the frequency of “slips of action” - irrelevant actions given the current circumstances but automatically triggered by environmental cues (De Wit et al., 2012). The slips of action manifest the previously acquired niche that has not been updated yet.

The above protocols “diagnose” habits when an affordance no longer meets its trained surroundings. If not for the change in the surroundings, the circumstances would guide affordance toward the known future and would be understood as exploitative affordance in the niche. For example, one might say that he automated coffee affordance in a specific office location. Still, when the coffee machine changes place – one would be called having a *habit* of getting the coffee at this particular place as the affordance is repeated despite the broken relationship between an action and its consequence. Action considered goal-oriented in one circumstance suddenly becomes interpreted as a habit due to a change in the surroundings, not a change in the information processing system.

The system acts on its model, and at the moment of initiation of the affordance, the system anticipates the usual reliability of the model. In this light, the critical characteristic of the habitual action is not teleological, but that such action is automatically *elicited* by a cue based on a cached value. In other words, action is habitual when exploitative, i.e., the experience of specific affordance guides its initiation.

Subsequently, studies on instrumental learning moved toward computational neuroscience. They were realized as flexible Model-Based (MB) and habitual Model-Free (MF) controllers (Daw et al., 2005; Doya, 1999; Doya et al., 2002; Smittenaar et al., 2013; Sutton & Barto, 2018). Further research focused on investigating cooperation and competition between the controllers (Daw et al., 2011; Doll et al., 2009; Fermin et al., 2010; Gershman et al., 2012; Gläscher et al., 2010; Otto et al., 2013; Simon & Daw, 2011; Wunderlich, Dayan, et al., 2012; Wunderlich, Smittenaar, et al., 2012, for a review see (Dolan & Dayan, 2013)). Despite various operationalizations, this line of research recognizes a division between two ends of a spectrum of decision-making: the MB controller, which is computationally expensive, deliberative, and flexible, and the MF controller, which is computationally efficient, automatized, and inflexible. Actions result from balancing these controllers' cooperating and competing simultaneous activity. Here, the MF habitual controller encapsulates minimal free energy as the action consequences are cached at the initiation (see Section 4.4).

The reviewed studies indicate that acquiring skills and habits involves explorative following of the affordances toward the possible futures. Frequently followed affordances return familiar feedback and constitute an organism's niche. The labels of "habits" and "goal-oriented" actions are tremendously misleading as the criteria are not teleological but relate to the automaticity of eliciting the behavior. The acquisition of a skill is reflected as a transition of information processing between the brain's networks and demonstrates a shift from the explorable environment toward the exploitable niche. In general, it is noticed that the common focus of research on actions, habits, skills, and niche construction is that behavioral procedures become increasingly automated along subsequent repetitions, and such automation is reflected in accurate anticipations of the future. The landscape of potential futures encloses the experience of affordances that lead to the exploration of novel futures and these leading to the exploitation of the known futures. The entire experience of hierarchically organized affordances toward the potential futures is called here the surroundings.

## 2.4 Decision-making and action execution in the striatum

The research on instrumental conditioning dates back to research on cognitive maps by Tolman (1948) and stimulus-response accounts by Thorndike (1898) (see Section 2.3). Subsequently, this research line differentiated between goal-oriented and habitual actions. Goal-oriented actions “(I)reflect the relationship between the action and its effect (response-outcome control), and (II) the outcome should be desirable at the moment of choice” (Dolan and Dayan, 2013, p. 314). On the other hand, habitual actions rely on repeating the steps that have led to desirable outcomes but are currently divorced from the associated consequences (*ibid.*). However, the terminology implies teleological criteria for action, which is misleading. During the progress in the field, the language for researching goal-oriented and habitual actions has been directly adopted from the animal literature (Dolan and Dayan, 2013) without recognizing the complexity of human motivations, such as contradictory desires and complex intentions. Human agents build coherent preferences toward future actions (Hartnett et al., 2016; Pacherie, 2008). Action plans often span long into the future, revealing a mereological hierarchy in which an event consists of subevents with corresponding subgoals (Zacks et al., 2001, 2007; Zacks & Tversky, 2001). This suggests that actions are heterogeneous. They are hierarchically organized and differ in length and complexity.

Neuroscientific studies on information processing behind exploring and exploiting affordances investigate the process of action acquisition and execution in the basal ganglia (BG) (Poldrack & Packard, 2003). The BG is a set of deeply located brain areas whose role is to gate the activity of the whole neocortex (Rolls, 2016). The central part of the BG is the striatum (STR), a structure between the thalamus and cingulate cortex (Figure 11a). The STR constitutes one of the most critical animal networks that orchestrate the activity of the whole neocortex by inhibiting the thalamus (McCutcheon et al., 2021). Further, the STR is closely connected to the reward-motivated motivational circuits of the brain (Loonen & Ivanova, 2015), as well as the rhythmic clock of the brain (Breska & Ivry, 2018). The BG is involved not only in mediating movement per se, given the findings related to Parkinson’s Disease, but also in influencing information processing beyond locomotion, such as flexible navigation or emotional processes.

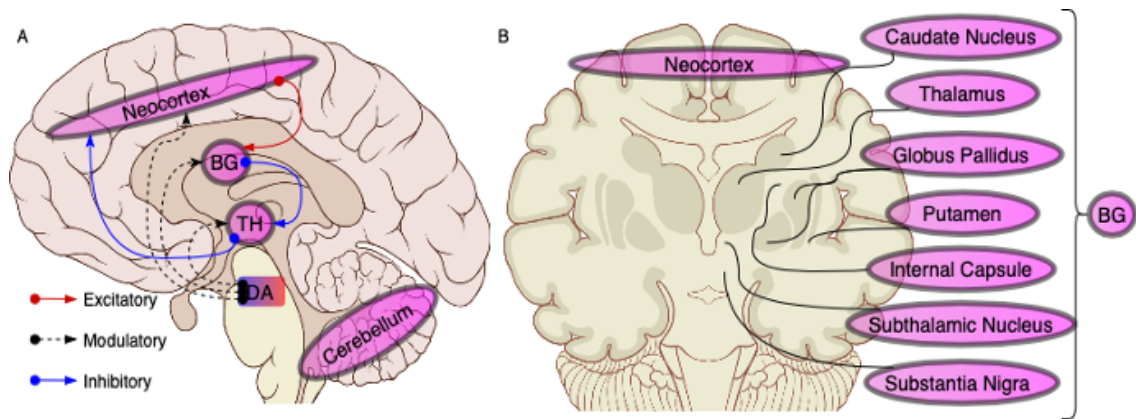


Figure 11. Simplified neuroanatomical organization of the brain. **A)** Sagittal section of the brain. The neocortex sends an excitatory signal to the respective parts of the Basal Ganglia (BG), which sends an inhibitory signal to the Thalamus (TH). As an effect, TH cannot inhibit the respective parts of the neocortex. The circuitry is modulated by the Dopamine (DA) from midbrain nuclei. Cerebellum participates in action control, albeit its role is beyond this work. **B)** Coronal section of the brain with components of the BG: Caudate Nucleus, Globus Pallidus [internal and external], Putamen, Subthalamic Nucleus (approximate location), and Substantia Nigra pars reticulata (approximate location). Internal Capsule is a white matter tract dividing the Caudate Nucleus and Putamen. The Figure is based on: (Goodroe et al., 2018a; Graff-Radford et al., 2017).

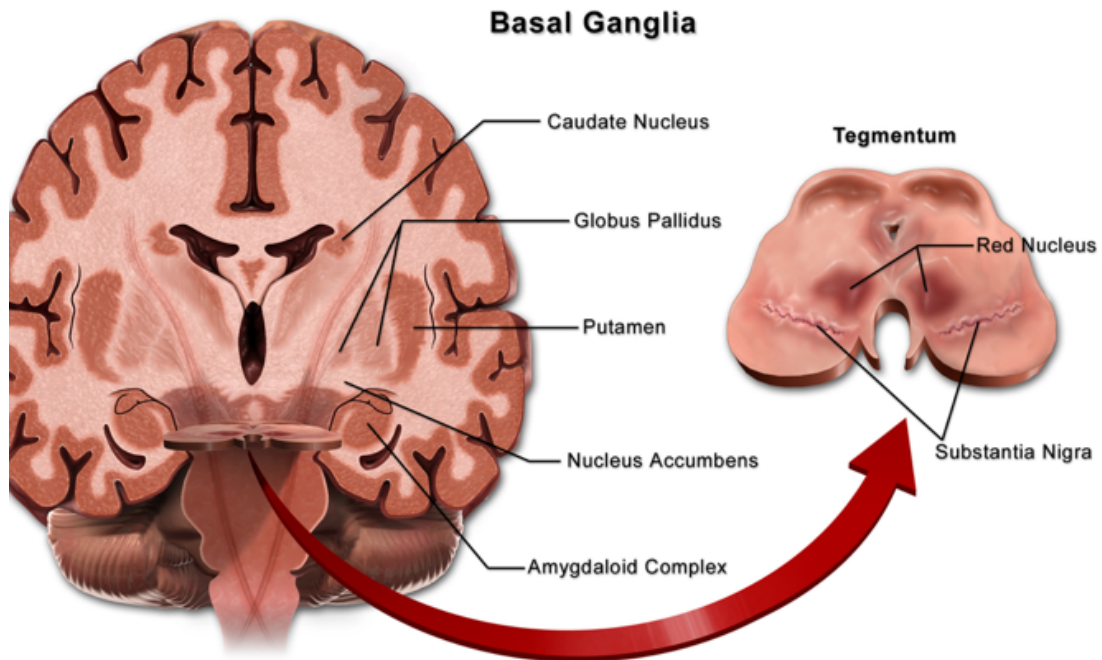
The STR in primates can be anatomically divided into the caudate nucleus and the nucleus accumbens, separated from the putamen by a white matter tract known as the internal capsule (Figure 11b). In rodents, the internal capsule does not separate the complex; thus, the STR is divided into dorsomedial, ventral, and dorsolateral. Studies show a gradient of information processing through the STR complex: from ventromedial parts mediating flexible behavior to lateral parts processing habitual behavior (DeCoteau et al., 2007; Devan & White, 1999; Ragozzino, 2002; Thorn et al., 2010)<sup>3</sup>.

The information processing in the STR is significantly influenced by dopaminergic modulation from the Substantia Nigra (SN) and Ventral Tegmental Area (VTA) (Figure 12) (see Section 6.2). Initial research on the dopaminergic nuclei was heavily influenced by movement disorders observed in Parkinson's Disease patients, whose dopaminergic neurons in lateral substantia nigra progressively degenerate (Duke et al., 2007). Medial and ventral portions of the substantia nigra project to different parts of the basal ganglia (McCutcheon et al., 2021; Y. Zhang et al., 2017) and are less involved in the disease progression. Just above the substantia nigra a second dopaminergic nucleus

<sup>3</sup> The same gradient is present in the midbrain dopaminergic nuclei, from ventrolateral Substantia Nigra (SN) through dorsomedial SN to Ventral Tegmental Area (Bromberg-Martin et al., 2010; A. P. Chen et al., 2021; McCutcheon et al., 2019, 2021).

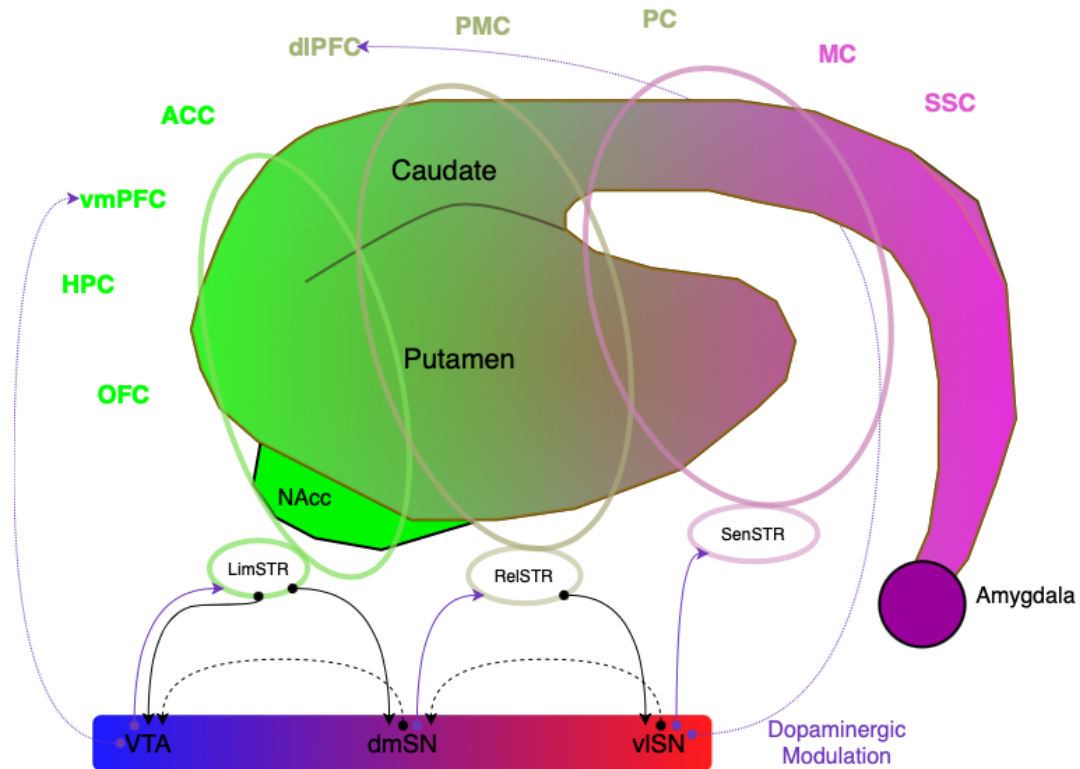


is located – the ventral tegmental area, which projects to its respective parts of the STR and neocortex (Bromberg-Martin et al., 2010). The SN, VTA, and STR are vital information processing components behind the following affordances.



**Figure 12. Selected subcortical structures involved in producing action acquisition and execution.** The substantia nigra (SN) and neighboring ventral tegmental area (VTA) (not shown in the figure) synthesize dopamine for the whole brain (Bromberg-Martin et al., 2010), including the basal ganglia (BG) presented in the picture. Figure attributed to Blausen.com (2014).

The alternative division of the STR is functional, enclosing ventrally located limbic striatum (LimSTR), anteriorly located associative/relational striatum (RelSTR), and situated posteriorly sensorimotor striatum (SenSTR) (A. C. W. Smith et al., 2021) (**Figure 13**). This functional operationalization is favored, given reports of involvement of the SenSTR in encodings (via D1-receptors in the Medium Spiny Neurons) and executing (via D2-receptors in the Medium Spiny Neurons) habitual behaviors (A. C. W. Smith et al., 2021). Since these observations have been performed only recently, the STR complex in earlier literature is divided anatomically rather than functionally.



**Figure 13. Human striatum and associated areas.** A schematic figure of the pathways of information processing in the STR of primates. The complex can be divided neuroanatomically in primates into the caudate nucleus, the putamen, and the nucleus accumbens. The complex is divided functionally in rodents into dorsolateral, dorsomedial, and ventral striatum. The division of the striatum adopted here is functional and conceptualized as Limbic (LimSTR), Relational (RelSTR), and Sensorimotor (SenSTR). The sections of the STR receive projections from various parts of the neocortex (indicated by color), are bidirectionally connected with dopaminergic nuclei in the midbrain, and send axonal projections to the respective sections of the thalamus (not shown in the figure). VTA = Ventral Tegmental Area, dmSN = dorsomedial Substantia Nigra, vLSN = ventrolateral Substantia Nigra, NAcc = Nucleus Accumbens, OFC = Orbitofrontal Cortex, HPC = Hippocampus, vmPFC = ventromedial Prefrontal Cortex, ACC = Anterior Cingulate Cortex, dIPFC = dorsolateral Prefrontal Cortex, PMC = Premotor Cortex, PC = Parietal Cortex, MC = Motor Cortex, SSC = Somatosensory Cortex. Based on: (Ferré et al., 2018; Goodroe et al., 2018a; Graff-Radford et al., 2017; Hooks et al., 2018; Lanciego et al., 2012; McCutcheon et al., 2019; Sherman, 2017; Xia et al., 2011).

Existing studies on rodents indicate that the RelSTR supports information processing associated with flexible behavior, whereas the SenSTR mediates information processing linked to inflexible behaviors (Balleine, 2005; Yin et al., 2005). Lesions to the RelSTR promote habit formation (understood as the action inflexibility, “response strategy”). In contrast, lesions to the SenSTR result in the maintenance of goal-directed (flexible, “place strategy”) behavior even with extensive training (Yin & Knowlton, 2006). Studies on mice show that associative loops through RelSTR modulate access to sensorimotor loops through SenSTR (Thorn et al., 2010). Recent studies in mice

correlated the activity of a cluster of neurons in the SN with initiating a movement sequence in a free exploration paradigm (da Silva et al., 2018). During skill acquisition, the computation in the RelSTR is attenuated, and the information processing in the SenSTR begins to bracket the entire sequence (K. S. Smith & Graybiel, 2013; Thorn et al., 2010); for a review, see (Graybiel & Grafton, 2015). A transition from the RelSTR toward the SenSTR has been observed during training skills in mice (Yin & Knowlton, 2006) and primates (Brotchie et al., 1991; Kermadi et al., 1993; Z. M. Williams & Eskandar, 2006). The RelSTR modulates the activity of the associative parts of the cortex, being a vital part of the associative learning processes.

The SenSTR is considered a hub of the “knowledge how” memory system and cooperates with the parietal cortex and the primary sensory cortices, in particular with motor and somatosensory cortices (Poldrack & Packard, 2003; Tricomi et al., 2009; Yin et al., 2005). The SenSTR is tightly connected with the motor cortex, which indicates building an enduring representation of the motor sequence (Coynel et al., 2010; Lehericy et al., 2005). The acquisition and automation of skills are reflected in a transition of information processing between these structures (Poldrack & Packard, 2003; Williams & Eskandar, 2006; Yin & Knowlton, 2006). Initial attempts to perform a skill engage the spatial (associative) format of deciding what to do and how to do it, while after a sufficient amount of practice, the skill reflects efficiently obtaining an outcome with trained motor representation (Hikosaka et al., 2002). These studies are explored further in Chapter 6.

The activity of the STR slices a continuous experience into discrete chunks in a process named bracketing (K. S. Smith & Graybiel, 2013; Thorn et al., 2010). The process is well documented in rodents, yet as Graybiel and Grafton (2015, p. 5) notice: “*the function of bracketing remains unknown*”. Here, bracketing is interpreted as a neural manifestation of the length of a transition in time. It is impossible to pinpoint how long an action is, as actions chunk together (Balleine, 2005; Desrochers et al., 2016; Dezfouli et al., 2014). From a particular state (i.e., at home), a handful of affordances can be followed (i.e., walking a dog, going to work, cleaning). The remaining part is habitually elicited once an action is initiated (i.e., leashing a dog, grabbing a suitcase or a vacuum cleaner). Thus, after initiation, exploitative affordances usually require no decision-making as perceiving a cue automatically elicits the remaining part of the exploitative affordance without considering alternative decisions.

## 2.5 Summary

Animals are understood as agents acting upon their subjectively experienced surroundings. Executing actions implies following affordances, which results in an experience of subsequent expected and surprising affordances. The affordances are distributed on the exploration-exploitation continuum. Explorative affordances are investigated as goal-directed actions, open skills, initial stages of skill acquisition, and the MB controller; they are associated with information processing in the RelSTR. Exploitative affordances are investigated as habitual actions, closed skills, autonomous stages of skill acquisition, and the MF controller; they are associated with information processing in the SenSTR. Animals experience the hierarchical landscape of affordances toward potential futures that span the exploration-exploitation spectrum as exploitative niches and explorative environments that jointly compose surroundings. However, the evidence suggests that the information processing in the above structures is insufficient to compute the phenomenological experience.

### 3. Information processing behind the conscious experience

Animals phenomenologically experience possibilities for actions known as affordances. There is *something like* having a specific experience given one's phylogenetic and ontogenetic history (Nagel, 1974). In this chapter, the phenomenological experience is specified as a conscious, coherent, and effortless experience of the meaning of the situation associated with information processing in a set of brain areas collectively called the gestalt cortex. The experience of qualia encompasses a broad spectrum of possible construals, including matter, minds, meaning, and emotions, from which this work focuses on the action-oriented qualia known as affordances. Specifying the information processing behind the phenomenological experience allows for more precise operationalization of the subset of qualia related to actions.

### 3.1 Conscious, coherent, effortless experience of subjective construal

The phenomenological experience of qualia encompasses a rich spectrum of phenomena. Out of all possible experiences, this work is interested in action-oriented qualia (affordances) that correspond to changes in the sensory, somatosensory, and vestibular flows of information. The experience of the meaning of a situation is known in social psychology and linguistics as construal (Frazier & Clifton, 1996; Geeraerts, 2006). This immediate interpretation of information can be quickly updated, and then a new construal provides a way of understanding the world by a specific being (subject of conceptualization) (Verhagen, 2010). In a sense, construals are the consciously experienced surroundings explaining the incoming information and guiding future actions.

The conscious experience is carefully analyzed by Lieberman (2022), who operationalized **experience as a conscious, coherent, effortless experience of subjective construal**. Such a definition of the experience is what stream of consciousness is (James, 2007). The experience is conscious as it is experienced, which is used as a synonym for “consciousness” (Tononi & Koch, 2015). Coherence means that at a given time, a single construal is experienced. Effortlessness implies that the experience of construal is readily present to the experiencing animals, and no deliberate effort is required for experience.

By contrasting effortless experience with effortful thinking, Liberman (2022) draws a boundary that thoughts are separate from experience. This division corresponds to experiencing the information processing correlated with the inputs and experience of the information processing dissociated from the ongoing flow of information. This dissociation is recognized in the literature as the difference between “experiencing self” and “remembering self” (Kahneman & Riis, 2005; Zajchowski et al., 2017). The experiencing self is immersed in the online flow of sensory, somatosensory, and vestibular information; the remembering self exists in dissociation from these channels, commonly called the mind.

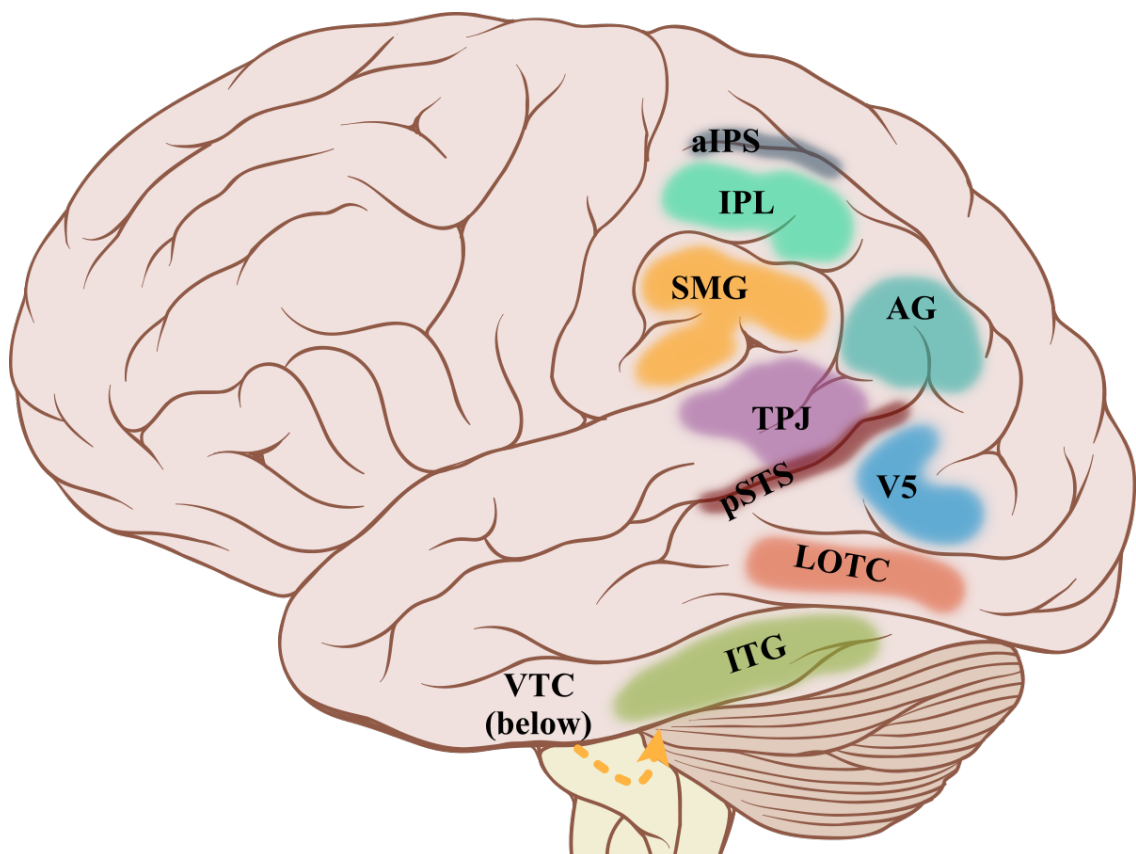
The sharp division between effortful conscious thought and effortless conscious experience presented by Lieberman (2022) suggests that these activities are mutually exclusive. However, thoughts, albeit effortful to generate, result in discovering new ideas that are themselves *experienced*. For example, watching a movie makes a person experience the plot, which can be effortfully reflected on by analyzing its flaws; in this

case, the content of experience is one's reflection on the plot, not the plot itself. Another example is imagination as a reflective (effortful) process capable of eliciting pre-reflective (effortless) experience of the imagined scenes, such as in the case of patient Shereshevsky, who was a master of a mnemonic technique called "memory palace" (Mecacci, 2013). This evidence points out that the "experiencing self" and "remembering self" are not mutually exclusive. Instead, these modes of information processing are intertwined as the content of experience may or may not relate to the incoming bodily information.

The experience content significantly differs between individuals and can originate from the processing of sensory, somatosensory, or vestibular information or the reflection dissociated from these inputs. Experience of imagination varies between individuals as certain people lack vividness in visual imagery (a condition called aphantasia) (Fulford et al., 2018), and people differ in their capacity to experience their episodic and autobiographical memory vividly (Boccia et al., 2019; Milton et al., 2021; Palombo et al., 2015, 2018; Watkins, 2018). This implies that the entirety of conscious experience is representational and varyingly correlates with the ongoing flow of incoming information (see Section 4.1).

### 3.2 Gestalt areas compute the experience

Neural correlates of experience are studied within theories investigating consciousness experimentally (Dehaene et al., 2014; Dehaene & Changeux, 2011; Koch et al., 2016; Siclari et al., 2017; Tononi et al., 2016), for a review see Seth and Bayne (2022). In his article, Lieberman (2022) addressed these theories and linked the experience of construal with the activity of a posteriorly located set of brain areas that he called the gestalt cortex (**Figure 14**). According to Lieberman, theories of consciousness include the gestalt cortex in their predictions about the neural correlates of consciousness. The name of this set of regions is a direct reference to gestalt psychology, which recognizes that the sum of the experience differs from its parts, similar to how the construal denotes a spatiotemporally coherent understanding of a specific situation.

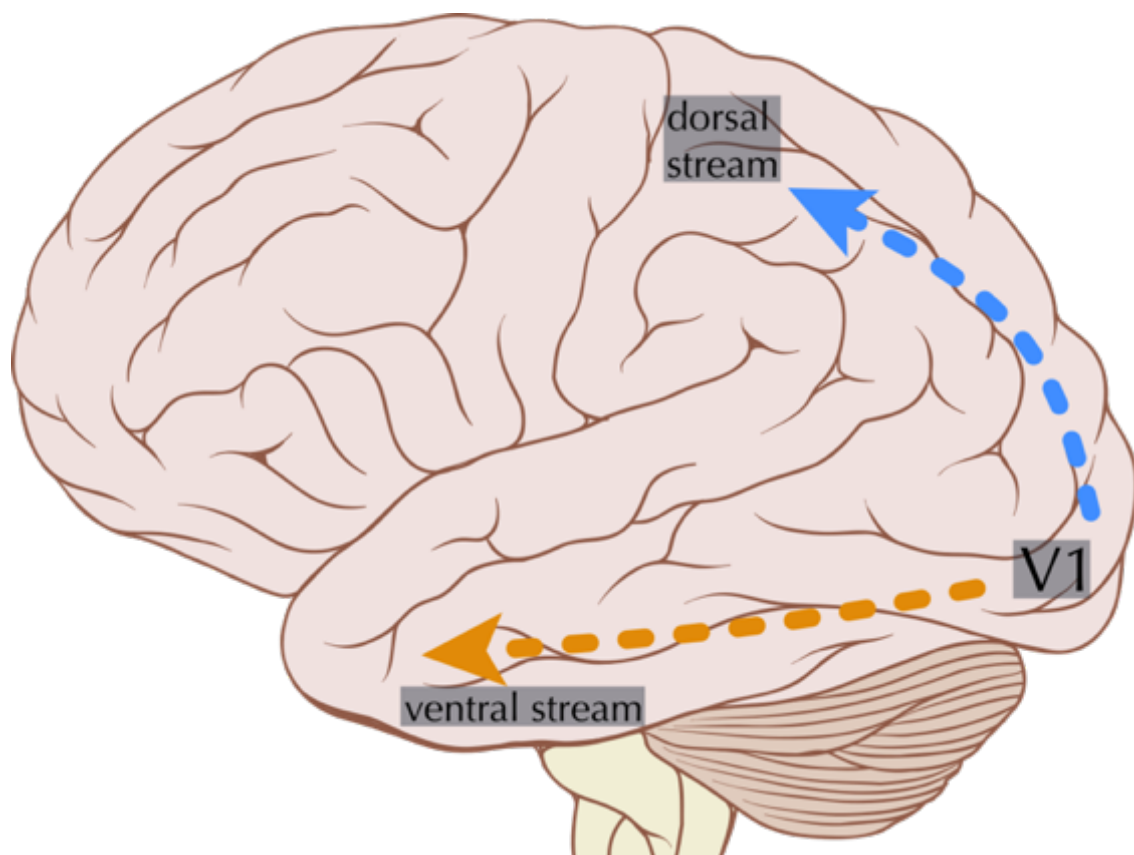


**Figure 14. Gestalt areas.** Areas suggested by Lieberman (2022) processing information behind the conscious, coherent, and effortless experience of the subjective construal. The similarity of experience is reflected in the neural synchrony of the gestalt cortex between subjects (for a review, see Lieberman, 2022; Yeshurun et al., 2021). aIPS – anterior intraparietal sulcus, IPL – inferior parietal lobule, SMG – supramarginal gyrus, AG – angular gyrus, TPJ – temporoparietal junction, pSTS – posterior superior



temporal sulcus, V5 – motion areas for objects and bodies, LOTC – lateral occipitotemporal cortex, ITG – inferior temporal gyrus, VTC – ventral temporal cortex (on the bottom of the brain). (The brain figure in this and every subsequent token of this figure is used according to Creative Commons Attribution 2.5.)

The localization of the gestalt areas reflect the fact that the human brain predominantly processes visual information. Visual information processing starts at the level of receptors on the retina, reaches the primary visual cortex through the thalamus, and diverges into two interconnected streams of visual information processing known as ventral and dorsal (Milner, 2017) (**Figure 15**).



**Figure 15. Ventral and dorsal streams.** Schematic illustration of the dorsal “where” and ventral “what” streams (Milner, 2017). Two streams are partly independent brain networks processing visual information in the primate brain. The ventral stream passes through the ventral temporal cortex and reaches the hippocampus; the dorsal stream terminates in the lateral portion of the inferior parietal lobule and the dorsolateral prefrontal associative area (Guterstam et al., 2015, 2018) Information processing in the ventral stream is qualitatively different at the retina level, from which parvocellular pathways to the lateral geniculate nucleus in the thalamus give rise to the ventral stream of information processing (Kravitz et al., 2013). Complementary, the magnocellular pathway between the retina and thalamus processes information relevant to the dorsal stream.

Information computed by the streams is intertwined at every level of processing, from the thalamus to associative regions of the neocortex. Thus, information processing within the streams is separate but still interconnected. Crucially, the ventral stream sharply differentiates the processing of animate and inanimate stimuli (Connolly et al., 2012; Thorat et al., 2019).

The ventral stream comprises, among other structures, the Ventral Temporal Cortex (VTC), which consists predominantly of the Fusiform Gyrus (FG), which is included in the gestalt cortex proposed by Lieberman (2022). The VTC organizes information processing along axes pointing to the animate-inanimate distinction. The FG is divided by the mid-fusiform fissure into two parts: the lateral portion is most active when processing faces, small objects, and living things, while the medial portion is most active when processing places, large objects, and non-living things (Grill-Spector & Weiner, 2014). Posterior portions of the VTC categorize experience based on perceptual features, whereas the anterior part of the VTC categorizes experience along the agency dimension (Thorat et al., 2019). Information processing in the ventral stream is contemporarily modeled with convolutional neural networks (Lindsay, 2021). This points to two parallel organizations of the VTC as a potential direction for further inquiry.

The VTC computes the early stages of information processing within the primate's ventral stream. The VTC uses a nested spatial hierarchy to organize representations of visual information, allowing for flexible access to category information at various levels of abstraction (Grill-Spector & Weiner, 2014). This spatial hierarchy serves as a neural infrastructure for the representational scale in the VTC, resembling the spatial organization of conceptual spaces developed in linguistics (Gärdenfors, 2014). The categories are organized from the basic level (e.g., car vs. face) to the superordinate level (animate vs. inanimate) to the subordinate level (Tom vs. Bill). Subsequent research showed that image categorization on the superordinate level occurs concerning categorizability and agency (Thorat et al., 2019). The categorizability is based on the separation of visual details into different dimensions. For example, face recognition in the FG is computed on an n-dimensional matrix of individual facial features (Chang & Tsao, 2017) that can be extrapolated into representing different matrices, such as cars (Burns et al., 2019). The agency is associated with the capacity for self-propelled motion, i.e., performing intentional actions (Shatek et al., 2022; Thorat et al., 2019). The neurobiological evidence shows that the VTC processes information within the ventral stream by categorizing the objects as either animate or inanimate

concerning the agency. Further, a recent electrocorticography (EcoG) study on epileptic patients showed that the ongoing experience of objects is underpinned by sustained activity within the VTC (Vishne et al., 2023).

Studies on the ventral visual pathway suggest that information processing in the VTC and the ITG compute the topological arrangement of continuous information about objects' form (Ishai et al., 1999). Further, the activity of right-lateralized AG and the left-lateralized ITG have been associated with visual recognition of patterns (Herath et al., 2001). The LOTC is involved in the mental imagery of body parts (Kikuchi et al., 2017). Evidence supports the view that components of the ventral stream process information related to objects' identity based on their perceived and remembered categories.

In the dorsal stream, the V5 processes information related to biological motion, that is, its presence and direction in both front-parallel (parallel to the face) and in-depth movement (Zeki, 2015). The pSTS located next to the V5 processes information about the outcome of human and non-human intentional behavior (Shultz et al., 2011). Thus, this region combines expectations of the most likely course of action given the action's inferred meaning (Stehr et al., 2021).

The AG located dorsally to the V5 computes various information associated primarily with semantic processing (Binder et al., 2009; Bonner et al., 2013). Damage to the AG results in the angular syndrome characterized by alexia (incapacity to recognize words) and agraphia (incapacity to write words) (Nagaratnam et al., 2002). The AG is further functionally divided into components that show different activities depending on task demands (Seghier et al., 2010).

The AG located rostrally the SMG shows high lateralization of functions, resulting from language processing. In most people, language comprehension (Wernicke's area in the STG) and production (Broca's area in the IFG) are left-lateralized. As a result, the left-lateralized SMG supports word processing (Oberhuber et al., 2016) and pitch memory (Schaal et al., 2017). In contrast, the right SMG is involved in the processing of rhythm in speech (Schaal et al., 2017), proprioceptive signals (Ben-Shabat et al., 2015), emotion recognition (Wada et al., 2021), and empathy (Silani et al., 2013).

Lateralization is also observed in the TPJ located ventrally to the SMG and AG. Left TPJ is involved in inferences in strategic decision-making, while the right TPJ in the detection of human agency (Ogawa & Kameda, 2019), embodied perspective-taking (Martin et al., 2020), moral conflict (Obeso et al., 2018), and emotional mimicry (Peng

et al., 2021). Some studies do not report on the functional lateralization of the TPJ and link bilateral information processing in this area with the conscious experience of the self (Blanke et al., 2005) and self-other distinction (Quesque & Brass, 2019), which supports the view that this area is involved in broadly understood social cognition, perspective taking, and attentional processes (Krall et al., 2015; Kubit & Jack, 2013).

The IPL is involved in several functions, including spatial attention, multi-modal sensory integration, and oculomotor control (Clower et al., 2001). Its role is even broader as it includes processing information related to language and social processing (Numssen et al., 2021). Studies suggest the IPL is divided into three functionally separated segments (Caspers et al., 2013).

The IPS located dorsally to the IPL processes sensory and somatosensory information to control arm and eye movements in space (Grefkes & Fink, 2005). The IPS computes information underpinning working memory tasks contralaterally, similar to the organization of the early visual areas (Bray et al., 2015). Studies on humans show that the IPS plays a crucial role in response inhibition (Osada et al., 2019). This area is also heterogeneous and can be divided into subdivisions (Niu et al., 2020).

The gestalt areas suggested by Lieberman (2022) located in the parietal cortex (aIPS, IPL, SMG, AG, TPJ) mediate conceptual, social, and spatial information processing. Lieberman's (2022) statement is that these areas and temporal regions are included in processing information underpinning conscious experience. This observation aligns with evolutionary evidence pointing to the parietal cortex's recent phylogenetic development (Iriki and Taoka, 2012). The hypothesis is that the expenditure of the parietal cortex correlates with the increasing complexity of the niche composed of physical objects and social interactions. Gestalt areas included highly expanding areas during the onto- and phylogenesis of *H. sapiens* (Fjell et al., 2015), further supporting the hypothesis that these areas' development constitutes an individual's conscious experience.

The activity in the gestalt areas tends to synchronize between subjects who experience a given situation from the same perspective. For example, listening to a narrative evokes similar between-subjects activity in the gestalt areas, even when presented in different languages (Honey et al., 2012). In another study, decoding the high dimensional structure of a narrative with language processing software allows for training a classifier capable of decrypting from neural data which story a given

participant is reading (Dehghani et al., 2017)<sup>4</sup>. Other studies suggest that memories about specific events share neural representation (J. Chen et al., 2017; Zadbood et al., 2017). These studies indicate that between-participant synchrony in gestalt areas reflects adopting the corresponding understanding behind the conscious experience.

Lastly, conscious experience should not be confused with the neural correlates of memory, such as the areas located medially to the VTC: the Parahippocampal Gyrus, the Entorhinal Cortex (EC), and the Hippocampus (HPC). These regions do not compute the information underlying the experience, given that the amnesic patients still experience it. Instead, studies involving epileptic patients have revealed that specific cells within the HPC, known as “concept cells,” are active when experiencing and imagining objects (Quiroga, 2012). These cells remain active during working memory tests, as shown by Kornblith et al. (2017). Crucially, the cells become sensitive to new items when presented with other things, as Reddy and Thorpe (2014) demonstrated. This evidence suggests that the information processing in these regions involves memory encoding related to the experience, not the experience itself. Further, this points to the observation that the conscious experience is distinctive to every single being as the content of experience differs between individuals.

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<sup>4</sup> Note that this article is co-authored by Ashish Vaswani, a main author of the “Attention is all you need” paper, which started the Transformer architecture and led to development of the large language models such as ChatGPT (Vaswani et al., 2017).

### 3.3 Summary

The studies reviewed in this chapter pinpointed the neural computations behind the conscious experience of subjective construal. The experience is defined as conscious, effortless, coherent, and subjective. The content of experience is a pre-reflective construal that denotes understanding a given situation given the background knowledge. In the human brain, the experience is associated with information processing in the gestalt areas, which varyingly correlates with the ongoing input. The gestalt areas synchrony point to the possibility of identifying an inter-subject neural underpinnings of the conscious experience. However, these areas do not work in isolation and communicate with other regions in the large-scale brain networks (see Section 5.2). Thus, the experience computed in the gestalt areas can originate directly from the incoming information or an effortful thinking process. In either case, the experience itself is effortless. Before reviewing the brain network involved in computing the content of experience, the research on memory systems is discussed, as memory captures one's identity and thus influences one's conscious experience of the construal.

#### 4. Two kinds of spaces for the future are stored in memory.

The principle of future-oriented information processing entails evolutionary pressure for developing memory to increase the accuracy of predictions, i.e., reducing future surprises. The principle is shared in many frameworks, most notably in the framework known as the free energy principle, which describes how organisms maintain their homeostasis by minimizing free energy through accurate predictions (Friston & Stephan, 2007). The free energy principle is considered a general imperative for self-organizing systems encapsulating what an organism should do to maintain its allostasis in the long run.

The free energy principle is unconnected to any biological/neural theory but is often linked to (I) Bayesian inference in the predictive coding theory (Friston, 2011; Knill & Pouget, 2004). Alternatively, the free energy principle relates to (II) ecological-enactive accounts, extending the principle to the whole brain-body-environment system (Bruineberg, Kiverstein, et al., 2018; Bruineberg & Rietveld, 2014; S. Gallagher & Bower, 2014). The ecological-enactive model is interpreted as computations of the biomechanical space; the Bayesian hierarchical generative model is understood as calculations of the inferred space. It is claimed that every agent performs multiple spatiotemporally broad actions in numerous biomechanical and inferred spaces. Parts of these spaces resonating with the gestalt areas are experienced in a subjective, conscious, effortless, and coherent manner.

Nevertheless, the spaces interact independently from the gestalt areas. The training of the biomechanical and inferred spaces takes place in a broader context of the entire brain's activity. The spaces are depictions of the computations performed in the specific brain networks. The brain networks undergo lifelong development and sophisticatedly interact with each other on structural and functional levels (Beaty et al., 2015; M. Chen et al., 2022; Garin et al., 2022; Huijbers et al., 2011; Uddin et al., 2019). To explore the architecture of the spaces, studies on the neurobiological basis of memory are reviewed. Notably, the brain network enclosing the hippocampus (HPC) is in focus as this network is investigated with the most scrutiny.

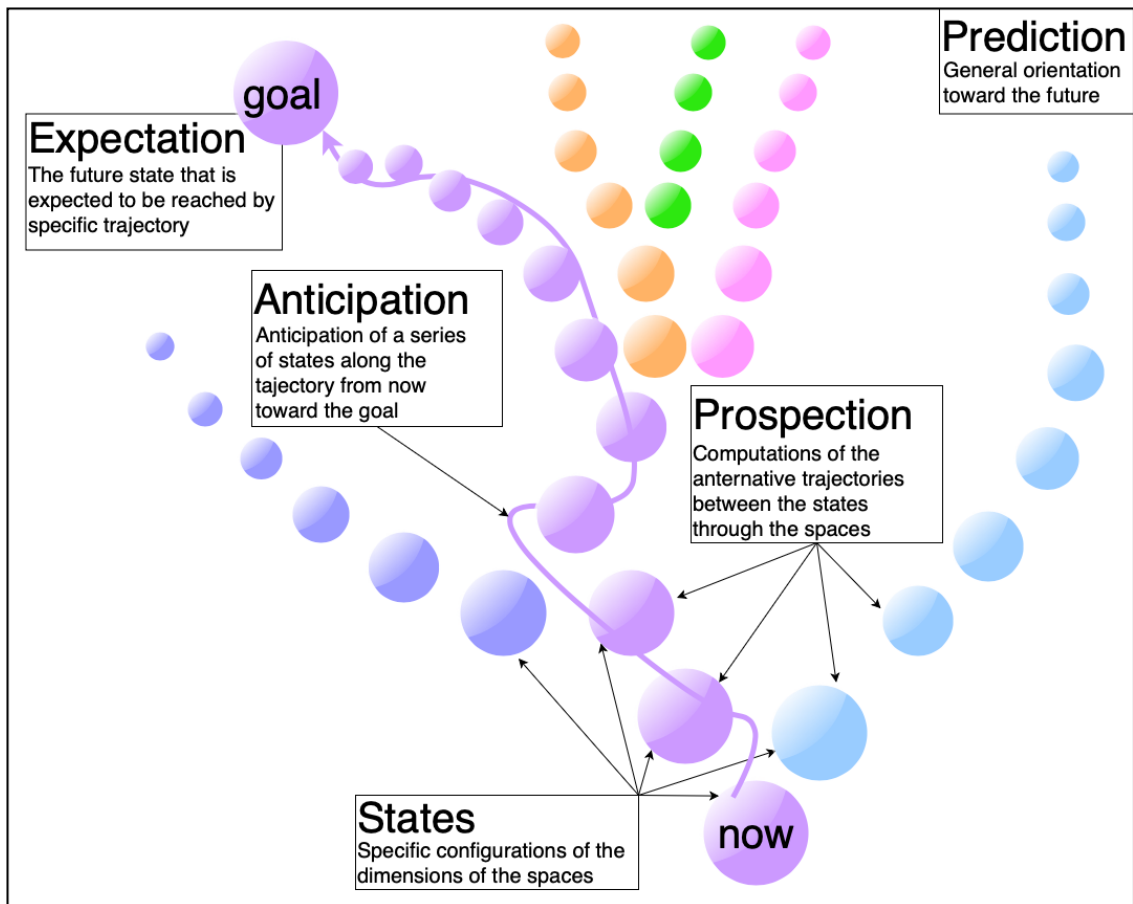
## 4.1 Two interpretations of the free energy principle

A wealth of literature acknowledges the importance of future-oriented information processing; here, the review starts with the free energy principle framework. Accounts of the predictive brain (Bruineberg, Kiverstein, et al., 2018; Constant et al., 2021; Friston & Stephan, 2007) agree that perception is fundamentally hypothesis testing (Gregory, 1968, 1980), which itself is an exemplification of perception as “unconscious inference” (Von Helmholtz, 1886). The proponents of the free energy principle posit that the principle encapsulates the organization of all self-adaptive systems (Friston et al., 2023). However, since its inception, the free energy principle has been interpreted in multiple ways, grounding the principle in numerous frameworks (Bruineberg, Kiverstein, et al., 2018; Bruineberg & Rietveld, 2014; Corcoran et al., 2020; Friston, 2013; Hohwy, 2016; Kiefer, 2020; Kirchhoff & Kiverstein, 2019; Safron, 2020, 2021). Also, the principle itself has been refined since the initial introduction (Andrews, 2021; Biehl et al., 2021; Da Costa et al., 2021; Friston, Da Costa, et al., 2021; Friston et al., 2023).

Proponents of the ecological-enactive implementation of the free energy principle argue that the anticipating brain is not a hypothesis-testing scientist (Bruineberg et al., 2018). This argumentation tackles animals as constructing generative models of the hidden causes of their experience (Friston and Stephan, 2007). Here, it is recognized that whether a given experience is classified as hypothesis testing strictly depends on the place of this affordance on the exploration-exploitation spectrum (see Section 2.3). Exploitative (known) affordances reflect hypotheses tested multiple times in the phylogenetic and ontogenetic past, are part of automated fixed action patterns, skills, or habits, are within the niche, and an animal anticipates the same outcome as always. Explorative (uncertain) affordances reflect novel hypotheses associated with goal-oriented actions within the environment, and an animal is unsure about the consequences. The interpretation here is that “testing” of exploitative affordances involves anticipation of familiar outcomes, whereas “testing” of explorative affordances necessarily entails uncertain outcomes.

The precise terminology must first be established to discuss the predictions for the future. This work uses the vocabulary suggested by Bubic (2010) (**Figure 16**).





**Figure 16. Future-oriented terminology.** Precise terms for talking about the future. The present moment is the current state of the space, understood as computations of the biomechanical and inferred spaces along the relevant dimensions. The dimensions of the spaces are operationalized in the following chapters (see Section 5.1). Prospection involves computing potential, counterfactual states that are possible within the boundaries of a given space. It can be considered counterfactual thinking, planning, or playing dynamic team sports. Anticipation reflects information flow that has been prospected and is now calculated along the prospected trajectory. Thus, anticipation implies that the agent aims at a specific future state of the space, which applies to prospective information processing. Reactive information processing calculates any change in the state without prospection of alternatives. Expectation denotes a particular state in the future that is prospected and aimed at. The expectation is anticipated to be obtained after implementing a prospected trajectory from the current state of the space. The broad orientation toward the future is captured with the term prediction (adapted from Bubic, 2010).

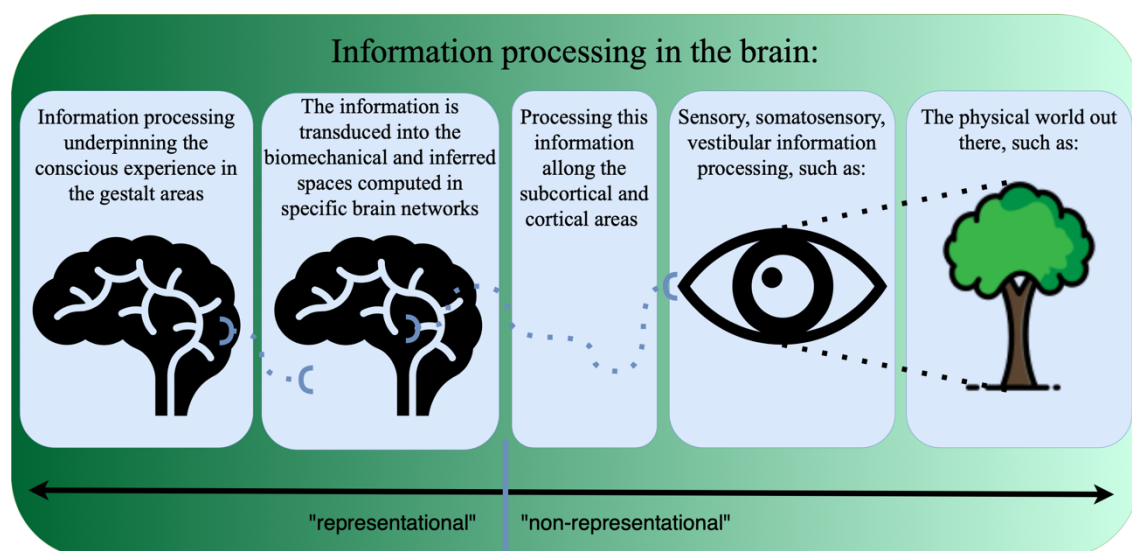
Agents broadly *predict* the future, *prospect* possible trajectories of the states, set *expectations* about the future states, and *anticipate* changes along the dimension of the space toward the expectations. Given the above terminology, the experienced surroundings of potential futures are anticipated expectations. During prospection, alternative expectations are computed and can be experienced with the involvement of the gestalt areas. Affordances entail processing expectations and anticipations together,

as affordances are anticipations toward an arbitrarily distant potential future (expectation). Along the transition in time, an organism processes the ongoing information and experiences novel, previously uncalculated future states and the affordances toward them (Pezzulo & Cisek, 2016). This navigation is necessarily hierarchical as the hierarchy organization of the entire information processing increases the accuracy of predictions and thus is evolutionarily favored. Following multiple affordances hierarchically is known as “having an optimal grip on a field of affordances” (Bruineberg & Rietveld, 2014, p. 1). Exploitable affordances in the niche require fewer computations as the alternative trajectories do not have to be calculated, and the anticipation covers the volatility within the closed skill (see Section 1.3).

The proponents of the free energy principle posit that future-oriented information processing applies to the entirety of the brain (Bruineberg, Kiverstein, et al., 2018; Constant et al., 2021; Friston & Stephan, 2007; Hohwy, 2015). Thus, the principle shall apply to information processing in the gestalt areas (surroundings of affordances) and other areas of the brain. The free energy principle makes no commitment to any particular theory of neural organization. However, it is often merged with Bayesian inference when describing the organization of living systems (Da Costa et al., 2021; Friston & Stephan, 2007). This, in turn, has been criticized by proponents of the ecological-enactive interpretation of the free energy principle (Bruineberg, Kiverstein, et al., 2018; Kirchhoff & Kiverstein, 2021), who posit that the principle is better suited to “anti-representational” (ecological-enactive) accounts of cognition. Soon later, Constant, Clark, and Friston (2021) published an article accepting both implementations of the free energy principle, which they call “representational” and “dynamicists”. In their paper, the authors argue that the former entails mental manipulations about symbolic representations, whereas the latter entails embodied interactions between the organism and its environment; thus, it excludes the intermediate representations. This notion is inspired by Gładziejewski (2016), who advocated that the free energy principle combined with Bayesian inference is representational. In contrast, the ecological-enactive accounts are considered anti-representationalist, given that, according to Ramesy (2007), the biological receptors conveying the information about the physical world do not satisfy the notion of representations.

Distinguishing between information processing in different brain networks adds layers of complexity to this issue. Namely, processing of the sensory, somatosensory, and vestibular information is as much “non-representational” as it can be, given how the

quantum information hits the biological receptors and the information is subsequently propagated along the axons of the receptor cells. Subsequent stages of information processing are gradually more “representational” as the information becomes transduced along the synapses and is gradually compressed/categorized/modified along the way (Figure 17). Here, the subsequent processing of information is understood as computing the biomechanical and inferred spaces, which are understood as representational. When the information reaches the gestalt areas, it computes the conscious, effortless, and pre-reflective experience of the subjective construal that is necessarily representational (see Section 3.2). Whether the early information processing is called representational or not remains to be argued by philosophers. Here it is accepted that the information processing occurring in the biological system is “representational,” at least from the stage at which it is composed into biomechanical and inferred spaces.



**Figure 17. Representational and non-representational information processing.** The information reaching the body (sensory, somatosensory, and vestibular) is as non-representational as it can be, given that the receptors operate on a quantum scale. Thus, some researchers accept that this information does not satisfy the criteria of representations (Constant et al., 2021; Gładziejewski, 2016; Ramsey, 2007). However, the information is progressively processed in the large-scale brain networks computing biomechanical and inferred spaces that are understood here as operating on the representational format. Subsequently, the spaces are consciously experienced when coupled with the gestalt areas.

The difference between the Bayesian and ecological-enactive implementations of the free energy principle is operationalized here in terms of two kinds of beliefs that a system implements. (1) Firstly, beliefs may reflect the *existence* of the physical objects generating the sensory, somatosensory, and vestibular flow of information. The objects

exist, but the information about this existence that reaches the nervous system is a representation, i.e., trees, ocean waves, or written physical equations are representations of objects (the hidden causes) generating input information. (2) Secondly, beliefs may point to *causes* beyond the online flow of the sensory, somatosensory, and vestibular information, i.e., originate from information processing in time (i.e., background knowledge). For example, the knowledge that Sally moved Ann's doll explains the lack of the doll in the initial place in terms of inferred actions of other agents (the hidden causes). Thus, the beliefs about the hidden causes are understood equivocally as either objects generating the information or inferences about why specific information has been generated.

To avoid calling one framework “representational” and the other “dynamic” when, in fact, both frameworks point to “representational” information processing, the frameworks are differentiated by specific information that they process. The former framework is associated with perception as unconscious inference (Von Helmholtz, 1886) refined later into perception as hypothesis testing (Friston & Stephan, 2007; Gregory, 1968, 1980). The latter framework treats the organism as a dynamic brain-body-environment system (Beer, 2008; Bruineberg, Rietveld, et al., 2018; Chemero, 2009; Varela et al., 2017). However, these studies do not specify what stage of information processing they refer to. In fact, the relevant literature often applies the free energy principle to the whole organism that processes information (Bruineberg, Kiverstein, et al., 2018; A. Clark, 2013; Friston, 2011, 2013, 2018; Kirchhoff & Kiverstein, 2019, 2021; Seth, 2013).

To clarify the terminology, this work assumes that the “representational” account denotes computing the inferred space in the specific brain networks, whereas the “dynamicist” account refers to calculating the biomechanical space in other brain networks. Both spaces are representational, albeit they model different information: (I) the latent causes explaining why the information is present and (II) the objects generating the ongoing information. In other words, the inferred space computes hypotheses explaining the flow of information, and the biomechanical space calculates the flow of the incoming information. The spaces shape each other in an organism's ontogeny in yet-to-be-explored interactions (see Section 5.3).

The information computed in the inferred and biomechanical spaces reaches the gestalt areas and is consciously experienced (see Section **Error! Reference source not found.**). The human's conscious experience differs tremendously in access to the

information that can be experienced due to many factors, for example, the differences in the sensory receptors resolution, neurodivergence, synesthesia, aphantasia, or endocrine system activity. The border at which the early information processing can no longer be experienced is also individual and cannot be drawn. At some point, information originating from the history of interactions between the computations of the biomechanical and inferred spaces reaches the gestalt areas and is experienced.

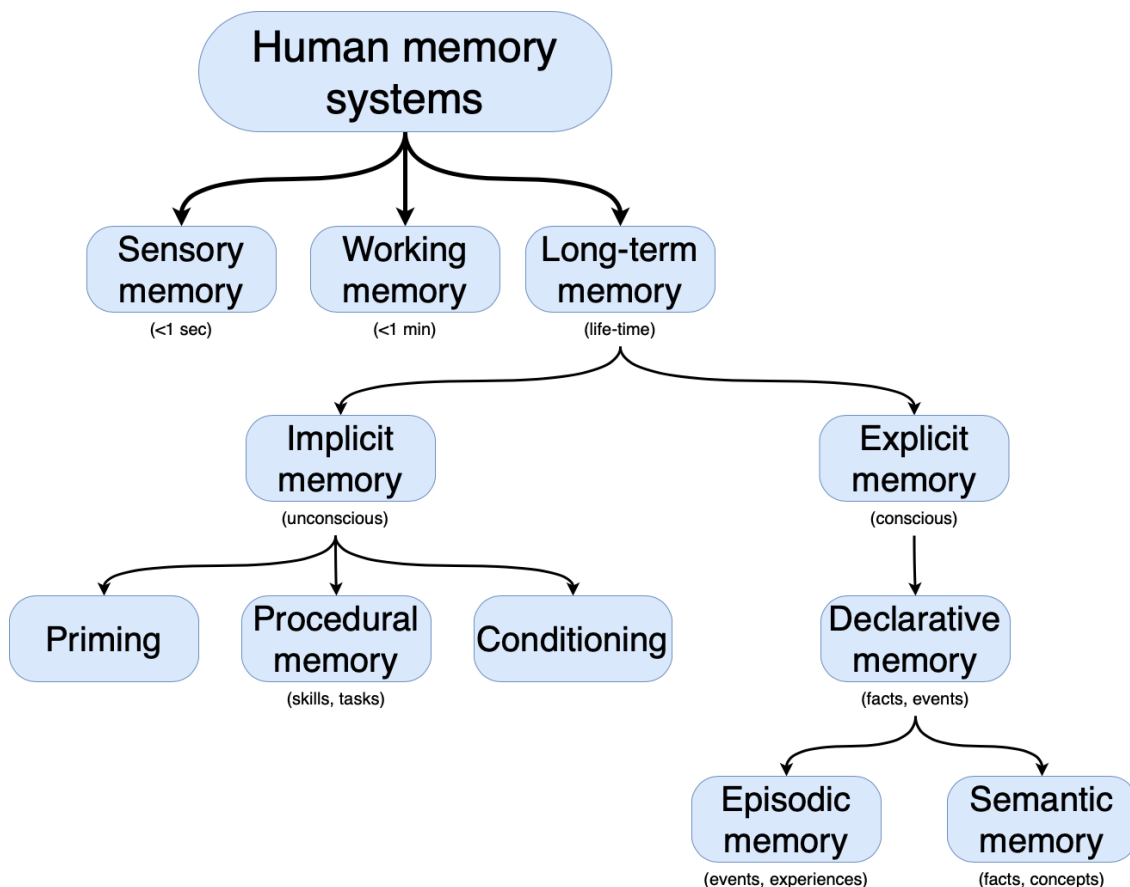
For example, experiments on information processing in the brain show that participants need around 50 ms after stimulus presentation to report its meaning reliably. However, photos displayed for as little as 13 milliseconds (ms) are recognized at a level better than chance (Potter et al., 2014). Further, studies on epileptic patients show that information processing for memory encoding needs around 300ms to reach the medial temporal lobe and the HPC (Kamiński et al., 2018; Quiroga, 2012) and around 500ms to reach the substantia nigra, which supposedly plays a vital role in encoding the information (Kamiński et al., 2018). These studies point out that the stimulus presentation, even for less than 50 ms, can be propagated in the information processing network and reach the gestalt areas several hundred milliseconds later.

The **orientation toward the future** is adopted as a general imperative of information processing in self-adaptive systems such as living organisms. From the receptors, the information is progressively transduced into biomechanical and inferred spaces and eventually reaches the gestalt areas that underpin conscious experience. The biomechanical space corresponds to the existence of objects generating the inputs; the inferred space corresponds to the hidden causes behind the inputs. Both spaces coexist under the general imperative of generating accurate future predictions. To further explore how the accuracy of anticipations is achieved, a review of memory systems is provided.

## 4.2 Two memory systems for encoding the statistical regularities

The free energy principle has been applied to biology makes an additional commitment to the Markov blankets, which is a statistical way of differentiating “internal states” from “external states” (A. Clark, 2017; Friston, Heins, et al., 2021; Hohwy, 2017; Pearl, 1998). The inside states hold “beliefs” about the outside states, understood as *hidden causes* behind the sensory experience (A. Clark, 2013; Friston & Stephan, 2007; Hohwy, 2020). Friston defines the “internal states” as holding probabilistic beliefs about the “external states” (Friston et al., 2023), thus internal states requires encoding and retrieval of information into memory.

In the broadest sense, memory points to the statistical regularities that a distributed information processing system manages to extract. In the second half of the XXth century, psychologists realized that memory can be divided into specific components. The initially developed model consists of sensory, working, and long-term memory (Squire, 1992) (**Figure 18**).



**Figure 18. Human memory systems.** The division of memory systems was suggested after decades of extensive psychological research. Contemporarily, the model is questioned in many ways: the labels shall include the ways of processing information instead of the division to implicit/conscious access (Henke,

2010); the entirety of memory is suggested to be procedural, i.e., consists of discrete series information (Keele et al., 2003); and the content of the declarative memory is proposed to be more sophisticated than a division to episodic and semantic memory suggests (Renoult et al., 2012, 2019).

Throughout the history of psychological research on memory, two types of long-term memory have been contrasted based on their respective abilities and limitations. The division into the two long-term memory systems starts from the famous case of patient H.M.<sup>5</sup> (Cohen & Squire, 1980; Squire, 2009a). Procedural memory relies on individual representations that are believed to be behaviorally expressed in an inflexible manner (knowledge „how”) (Eichenbaum, 2000; Packard, 2008). Declarative memory consists of relational representations and produces flexible behavior (knowledge „that”) (Eichenbaum, 2001). The hippocampus (HPC) is critical in dividing the memory systems, as suggested by Squire (1992), in his own words:

*Many terms have been used to describe a particular kind of memory (e.g., declarative, explicit, relational, or configural), and many other terms have also been used to describe a kind (or kinds) that are dissociable from the first kind (e.g., non-declarative, implicit, or habit). However, the terms themselves are not the proper focus. If one considers the various biological and purely psychological concepts that have been used, it is striking that they sort themselves out in terms of ideas about what the hippocampus does and does not do in the service of memory. It should not be surprising that these terms place themselves on either side of a biologically meaningful boundary. (Squire, 1992, p. 205)*

The HPC is one of the most extensively studied structures in the brain, yet details of its computations and its role in conscious experience are still mysterious. The quote above shows that the engagement of the HPC is required for one memory system but not the other. To understand the role of the HPC, its functions are reviewed.

Most notably, the HPC is associated with memory encoding, i.e., creating episodic memories or acquiring concepts. Researchers have been trying to pinpoint the neurobiological substrate of memory conceptualized as engram cells since Semon and Konorski, as summarized by Tonegawa (et al., 2015). Contemporarily, the enduring

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<sup>5</sup> The famous case of Henry Molaison, who due to epileptic seizures underwent bilateral lesion of hippocampi and adjacent structures in 1953. As a result, the patient lost capacity to create new episodic memories, albeit procedural memory remained intact (Squire, 2009).

neural changes resulting in memory encoding called engrams are defined as “*a population of neurons that are activated by learning, have enduring cellular changes as a consequence of learning, and whose reactivation by a part of the original stimuli delivered during learning results in memory recall.*” (Tonegawa et al., 2015, p.918). Experiments on mice led to the discovery of populations of cells created separately during contextual fear conditioning in the dentate gyrus of the HPC and the prefrontal cortex (Kitamura et al., 2017). A follow-up study revealed that the engram for a contextual fear conditioning memory is distributed across multiple brain regions (Roy et al., 2022)<sup>6</sup>. The distributed encoding of information about contextual fear conditioning reflects that this memory encloses multiple information channels computed in various brain networks.

Contemporary, one of the leading theories describing information processing in the HPC and the neighboring entorhinal cortex (EC) is the Tolman-Eichenbaum Machine (TEM) (Whittington et al., 2020). The TEM is an information processing system computing the structure of experience with the activity of the EC and combining this structure with sensory representations with the activity of the HPC. This line of research strongly suggests that the HPC and EC are involved in sequential, multidimensional information processing (Baldassano et al., 2017a). Albeit the information processing in the HPC is not necessarily required for the conscious experience, it contributes to its complexity by encoding the structure in the conscious experience into memory. For example, people developing Alzheimer’s Disease that corresponds to degeneration of the HPC still *experience*, yet the content of their experience is tremendously different.

Behavior observed in Alzheimer’s Disease points to the link between the hippocampus and navigation. Scientists who studied the animals’ HPC discovered cells active in specific regions of a maze called place cells (O’Keefe & Dostrovsky, 1971). Subsequent research revealed a hexagonal grid pattern representing the maze in the EC (Hafting et al., 2005; Moser et al., 2017). This discovery was awarded a Nobel Prize in 2014 and subsequently led to the discovery of a specialized navigational system in the HPC and EC (Fyhn et al., 2004; Hafting et al., 2005; O’Keefe, 1976; O’Keefe & Dostrovsky, 1971; Sargolini et al., 2006). Besides place and grid cells found respectively

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<sup>6</sup> These lines of research also show that the HPC mediates memory retrieval for two weeks after encoding. In contrast, retrieval after two weeks is mediated by the population in the prefrontal cortex of mice (Roy et al., 2017). Deactivating a part of the HPC known as the dorsal subiculum prevents memory retrieval with encoding remained intact.



in the HPC (Eichenbaum et al., 1999; O’Keefe, 1976) and the EC (Moser et al., 2008, 2017), other cells found in the HPC and adjacent structures are head-direction cells (Cullen & Taube, 2017), egocentric goal-direction cells (Hok et al., 2005; Sarel et al., 2017), egocentric object-vector cells (Høydal et al., 2019), speed cells (Kropff et al., 2015), border cells (Savelli et al., 2008; Solstad et al., 2008), boundary vector cells (Lever et al., 2009), and time cells (Pastalkova et al., 2008; Tsao et al., 2018). Further, the grid structure in the EC is sensitive to rewards and goals (Boccarda et al., 2019; Butler et al., 2019).

Complementary studies on humans record the activity of single cells in the HPC and advanced areas in the brains of epileptic patients (Quiroga, 2012). At the moment of creation of the concept cells (Quiroga, 2012), a theta-band activity over the prefrontal cortex of epileptic patients has been measured (Kamiński et al., 2018), presumably replicating the findings of the emergence of two distinct populations of engram cells at the moment of memory encoding (Roy, Kitamura, et al., 2017). Additionally, the phase-lock of theta band activity between the HPC and the OFC has been shown as causally underlying memory of the distribution of rewards (Knudsen & Wallis, 2020).

Further, recordings of epileptic patients revealed that successful formation of the concept cells involves the activity of putative dopaminergic cells in the substantia nigra pars compacta (SN) (Kamiński et al., 2018), which replicates finding about the dopaminergic influence on the memory encoding in the HPC identified in the rodents (Wagatsuma et al., 2018). These observations support the hypothesis that incorporating novel information into long-term memory is gated by dopaminergic influence on the HPC (Lisman & Grace, 2005) (see Section 6.2). Additionally, synchronization of the HPC and the prefrontal cortex during non-REM sleep has been suggested as a mechanism of memory consolidation (Lewis et al., 2018), supporting the findings from mice of maturation of the engram cells.

The HPC plays a crucial role in encoding the structure of a future-oriented, memory-guided, distributed information processing system. The HPC is essential for episodic memory, connecting “what” and “where” (Rolls & Xiang, 2006a; Tulving, 2002a), which can be rephrased as a conscious experience of counterfactual scenarios. An efficient information processing in the distributed system requires accurate memory of the experienced statistical regularities that guide subsequent predictions. The HPC slices a continuous stream of experience into distinct episodes (Ben-Yakov & Henson, 2018) via the activity of cells detecting time-boundaries of the episodes (Zheng et al.,

2022). The multidimensional associations reflect temporal succession of events (Friston & Buzsáki, 2016a), hierarchically organized over nested timescales (Baldassano et al., 2017a). This change in granularity of the timescales is presumably implemented along the long axis of the HPC, expressing a shift in the size of the place and grid cells' receptive fields (Bellmund et al., 2018; Collin et al., 2015a). These observations are supported by experimental observations of brain activity in the functional magnetic resonance imaging (fMRI), which showed that the HPC of people watching a movie reacted to event boundaries between the movie's scenes (Ben-Yakov and Henson, 2018). Some researchers suggest that the primary function of the HPC is to construct perceptual and abstract scenes (Maguire & Mullally, 2013). Such information processing organization satisfies the principle of future orientation because it promotes the hierarchical organization of the predicting models.

For example, recent studies have shown that the HPC stores experiences in the form of events, such as subsequent laps in a maze (Sun et al., 2020). Researchers have found a specific set of cells in the CA1 (the part of the HPC where place cells are identified) activated by subsequent laps. These “event-specific rate remapping” cells are shown to be independent of the activity of place cells. The authors conclude that investigated cells “*tracks the skeletal structure of experience via events as abstract entities, with abstract relationships between them.*” (Sun et al., 2020, p. 11). These observations suggest that the HPC is involved in identifying a transition between two states of the multidimensional, associative space.

The HPC-dependent networks have been related to navigating the physical and conceptual spaces (Bellmund et al., 2018; Gärdenfors, 2004, 2014), albeit this association does not capture the time dimension. The research reviewed above is understood in terms of the spatial organization of knowledge into exemplars of various categories and respective prototypes of these categories (Gärdenfors, 2014; Rosch & Mervis, 1975). The HPC-dependent networks involve pattern completion (including into a category) and pattern separation (dividing exemplars into different categories). Both pattern completion and pattern separation presumably occur in the HPC and are a bedrock of human cognitive abilities (Quiroga, 2020). Electrophysiological recordings on epileptic patients show that when moving anteriorly along the ventral stream, the categories become smaller and more concrete (Kamiński et al., 2018; R. Q. Quiroga, 2012). For example, the fusiform face area in the VTC has been shown to process the n-dimensional space of faces (Chang & Tsao, 2017; Quiroga, 2017), whereas the anterior portion of the temporal

lobe activates to a single exemplar denoting a unique, familiar face that is tied to the identity of the owner of the face (Landi et al., 2021).

The HPC-dependent networks have been suggested as a shared basis for memory, imagination, and future thinking (Mullally & Maguire, 2014), given the experiments showing that the computations in the HPC rely on constructing an experience of scenes (Maguire et al., 2016; Maguire & Mullally, 2013). Research on humans indicates that the HPC and the EC represent a self-location in actual space (Guterstam et al., 2015), as well as in hypothetical (counterfactual) spaces (Van Hoeck et al., 2015; Y. Xu & Corkin, 2001), and imagined spaces (Hassabis & Maguire, 2007a; Markman et al., 2009). Moreover, the HPC is a crucial hub for episodic memory, connecting “what” and “where” (Rolls & Xiang, 2006b; Tulving, 2002b), which can be rephrased as episodic imagination. The activity of the HPC slices a continuous stream of experience into distinct episodes (Ben-Yakov & Henson, 2018). This is related to the role of the HPC in organizing a temporal succession of events (Friston & Buzsáki, 2016b), as well as the hierarchical organization of the events over nested timescales (Baldassano et al., 2017b), presumably along the long axis of the HPC (Collin et al., 2015b). Overall, given the kind of computations that the HPC and the EC perform, it is suited for constructing a generative model (Friston, 2010; Goodroe et al., 2018) of the surroundings of potential futures. Navigating the rich landscape of affordances leading to potential futures involves experiencing counterfactual scenarios and making decisions. The reviewed evidence strongly suggests that the HPC is involved in processing information that contributes to such experiences.

Recall psychological research on skill acquisition, where skills are defined as sensorimotor or cognitive procedures (see Section 1.3). According to an original conceptualization, skill acquisition involves three phases: cognitive, associative, and autonomous (Fitts & Posner, 1967). The cognitive phase often goes beyond procedural memory and affects episodic and working memory (Ackerman and Cianciolo, 2000); thus, it involves computations performed in the HPC. Once the skill is learned, the involvement of the HPC is no longer required. In computational terms, skills acquisition relies on the MB controller, whereas autonomous processing is computed with the MF controller.

The skilled performance of the experts goes beyond the MF computations (Ericsson, 2006), as the exceptional abilities of experts, such as chess or baseball players, require cognitive management, which is generalized as navigating changing

environments, new situations, and uncertainty about competitors (Christensen et al., 2019). Expert performance in chess-like games is based on mastering the capacity to perceive a given situation and its development in time and implementing the right action policy, which requires information processing in the HPC. In psychology, skills are operationalized from straightforward sensorimotor procedures to skilled performance in complex environments, a broader operationalization than described here. Here, skills are exploitative chunks of information.

Complementary to the already reviewed studies, researchers of memory in educational settings distinguish the division between memory storage and memory retrieval (Bjork, 1988; Bjork & Bjork, 1992; S. M. Smith et al., 1978). The storage memory can be roughly thought of as accumulated associative learning that determines how easily retrieval is accessed and how robust it is. Retrieval memory determines what can be retrieved given the circumstances (cues, experience). This line of research shows that creating difficulties during learning, such as intertwined practice instead of block repetition or changes in the context of learning, results in weaker immediate retrieval, albeit better storage strength determining future retrieval (Bjork, 1988). After prolonged disuse, retrieval strength decreases, albeit it can be quickly reestablished (Bjork & Bjork, 1992). When surroundings are easily retrieved, no learning can occur, which reflects older ideas developed by Vygotsky, according to what learning relies on challenging oneself to reach beyond what is already learned (Del Río & Álvarez, 2007; Doolittle, 1997). One prediction of the theory is that storage strength becomes latent but never disappears (Bjork, 1988; Bjork & Bjork, 1992), which seems to be supported by recent studies on rodents (Roy, Muralidhar, et al., 2017). To further operationalize the information processing performed in the HPC and its respective phenomenological experience, the psychological models of memory are refined in the next section.

The HPC-dependent networks have been suggested as a shared basis for memory, imagination, and future thinking (Mullally & Maguire, 2014), given the experiments showing that the computations in the HPC rely on constructing an experience of scenes (Maguire & Mullally, 2013). Evidence indicates that the HPC's networks calculate self-location in physical space (Guterstam et al., 2015), hypothetical (counterfactual) spaces (Van Hoeck, 2015; Y. Xu & Corkin, 2001), and imagined spaces (Hassabis & Maguire, 2007b; Markman et al., 2009). For example, the research on the information processing underpinning the experience of natural scenes reveals that the scenes are perceived based on the statistical regularities in past experiences (De Cesare et al., 2017). Lauer and Vö

(2022) showed that the visual perception of natural scenes involves extracting *scene grammar* from the individual encounters of a particular view. The scene grammar is established by anchor objects, such as the fridge anchoring the kitchen-related items, the shower anchoring the bathroom-related things, and so on (Boettcher et al., 2018; Helbing et al., 2022) (Boettcher et al., 2018; Helbing et al., 2022). Johnson and Jonnson (2014) observed areas involved in visual scene perception and imagination, some overlapping with the gestalt areas (OPA, PPA, RSC, Precuneus/IPS).

### 4.3 The entirety of memory is procedural (i.e., discrete, sequential)

Understanding how the memory systems cooperate and compete requires realizing that the “declarative memory” is also procedural as it consists of discrete events. This realization has been made by Keele (et al., 2003), who suggested that all information processing in the brain is sequential. Memory systems can be described as “procedural” because they represent a series of events (chunks, transitions). Keele and colleagues differentiated between two systems processing information: a unidimensional system corresponding to the “memory how” and a multidimensional system corresponding to the “memory that”.

Empirical data support the theory developed by Keele and coauthors. Their evidence comes from psychological tasks such as the Serial Reaction Time (SRT), which measures implicit sequential learning (Curran & Keele, 1993). During this task, participants must respond to a series of stimuli presented in various modalities by giving specific responses (e.g., pressing one of four buttons). Each answer leads to the presentation of the next stimulus, which requires another reaction, and so on. Some participants are informed of the regularities in cues presentation, while others remain unaware. Some participants from the unaware group realize the regularity. Informed and uninformed but aware participants respond faster than unaware participants. After initial learning, a high or low-pitch sound played after each visual stimulus is added to subsequent blocks of the SRT. At the end of each block, the subjects were asked to report the number of high-pitched tones they heard. This introduction of the secondary task equalized the reaction times of participants from all three groups. This is interpreted as the engagement of the multidimensional system in the secondary task, so the first task is processed solely in the unidimensional system, revealing dissociation between the systems.

The findings indicate that two types of learning happen simultaneously during the initial training phase for a single task, which confirms that the memory systems work independently. In other experiments with the SRT task, subjects were divided into two groups practicing initially single-task or dual-task conditions. Participants learn better in single-task conditions compared to dual-task conditions. Nonetheless, all subjects performed comparatively when both groups were transferred into the dual-task condition. This implies that the secondary task inhibits the expression of the knowledge already

established in the multidimensional system, which shows that the memory systems compete.

Schmidtke and Heuer (1997) studied a version of the SRT task, where participants had to remember sequences of visual and auditory cues that occurred in 6-item sequences. They wanted to test whether learning of the sequences in either modality occurs independently or jointly by making the second task part of the same multidimensional sequence. The participants' reaction time indicates that the sequences bind together in the multidimensional system. However, after the shift in the initiation of the auditory sequence, the reaction time suggests that the unidimensional system processes the sequence again. Once the sequence shift in the secondary task breaks the correlation, the knowledge encoded in the multidimensional system is no longer viable. Another variant of the SRT reported in this study involved visual and auditory sequences of unequal length, yielding consistent observations.

These results were interpreted by Keele (et al., 2003) as showing that the multidimensional system creates inter-dimensional associations, whereas the unidimensional system creates intra-dimensional associations. According to Keele, unidimensional modules can extract separate representations only along a single dimension. These unidimensional modules respond only to input along a specific modality. The level of learning within these modules is not affected by whether they are trained under single-task or dual-task conditions. In the case of dual-task conditions, the amount of learning remains the same regardless of whether secondary events excluded by the module follow a random sequence, a sequence of unequal length, or a sequence of equal size. On the other hand, learning within the multidimensional system is more restricted. For this system to extract sequential associations, the successive events must either be in a single dimension or, if task-relevant information is present on multiple dimensions, the consecutive interdimensional events must be predictive. Observing the correlation between dimensions allows for extracting inter-dimensional associations with the multidimensional system, as explored in subsequent studies (Hsiao & Reber, 2001; Rah et al., 2000). The multidimensional predictability of following events reflects the real-world experience and encourages inter-dimensional learning. On the other hand, when circumstances are random, it discourages such learning.

In this line of research, dimensions are considered equal to separate modalities, albeit this distinction is an approximation. As Keele (et al., 2003) states:

*The issue of what constitutes a dimension is contentious and is reminiscent of an older issue in psychology about whether dimensions are separable or integral (e.g., Garner & Felfoldy, 1970). In the SRT task, the term dimension has generally been used interchangeably with modality, and we maintain this convention. However, stimulus attributes within a modality can also constitute relevant dimensions for sequence learning, similar to the way in which visual attention studies have described fundamental dimensions for perception (e.g., Treisman, 1988). Moreover, distinctions within the motor system (e.g., hands vs. feet) may also constitute dimensions. We expect that similar principles will apply across these various situations. (Keele et al., 2003, p. 317)*

Treating dimensions as modalities is a helpful simplification for the sake of experimental design. However, specific modalities (sight, hearing) have multiple dimensions that must be explored and specified. This understanding allows for seeing heuristics such as one-clever-rule (Gigerenzer & Gaissmaier, 2011) in a new light – as focusing on a single dimension. Dimensions are specified in the second chapter, where a living body is reduced to sensory, somatosensory, and vestibular channels of information flow. The channels are further divided into dimensions; for example, the somatosensory channel is roughly divided into pain, pressure, temperature, and proprioception information.

Keele's (et al., 2003) model provides a new perspective on Kamin's blocking effect, a phenomenon first described by Kamin (1969). This effect can be described with an experiment where, initially, a light is paired with a reward. Then, the light is presented with a new, not-associated stimulus, such as sound. Light and sound are jointly presented during training, and a reward follows. At some point, the sound is presented without the light. Presentation of the sound only does not produce a conditioned reaction. Keele's (et al., 2003) model proposes that the light-reward association is multidimensional and requires attentional resources. Therefore, when the sound is introduced, it is processed in the unidimensional system, which cannot make inter-dimensional associations. This implies making causal inter-dimensional associations that require attentional resources.

The division between uni- and multidimensional systems has been further developed by Gheysen and Fias (2012). They related inter-dimensional associations observed in the SRT tasks with HPC activation, whereas intra-dimensional associations with primary stimulus-specific cortices (occipital, motor, somatosensory). This division



neatly reflects the flow of sensory, somatosensory, and vestibular information corresponding to the biomechanical spaces and the information dissociated with these channels corresponding to the inferred spaces.

To summarize, various lines of research indicate that the HPC is involved in organizing the multidimensional experience into a form of discrete events. The suggested role of the HPC-EC system is constructing a navigational space at different levels of abstraction. The structure of the experience is provided with the computation done in the EC, whereas the HPC links multidimensional experience with this structure. Information processing in the HPC-EC by encoding and retrieving inter-dimensional associations is crucial for acting in the real world. Keele's work suggests that the intradimensional associations within the unidimensional system are processed independently by the early sensory cortices. These cortices are closely connected with SenSTR, validating Keele's insight about the role of the STR in computing the real-time conversion between sequence parts in a given action. The HPC activity has been tied to the multidimensional system, whereas basal ganglia (BG) mediated the activity of both uni- and multidimensional systems. The details of this information processing are investigated within computational neuroscience.

#### 4.4 The memory systems cooperate and compete

So far, it has been stated that memory-guided information processing in the future-oriented distributed system can be differentiated into uni- and multidimensional systems. The unidimensional system is associated with the biomechanical space and linked to information processing in the SenSTR. The multidimensional system is associated with the inferred space and related to information processing occurring in the HPC, EC, OFC, and RelSTR (see Sections 2.4 and 5.2). Both models process information procedurally and hierarchically, which implies that they consist of states, sub-states, and transitions between the states corresponding to the flow of information in the n-dimensional space. The biomechanical space is enclosed in the sensory, somatosensory, and vestibular dimensions; the inferred space is an abstract, n-dimensional space of arbitrarily extracted dimensions. This section builds on psychological and neuroscientific research on information processing and reports the computational framework of instrumental actions. This light provides a more detailed operationalization of the computational structure of the spaces.

Research on memory in psychology, neuroscience, and computational neuroscience suggests that the two memory systems process information simultaneously and independently (Dolan & Dayan, 2013; Geerts et al., 2020b; Poldrack & Packard, 2003; Squire, 1992). One system is known in the literature as relational, goal-oriented, multidimensional, and model-based, contrasted with the other system known as automatic, habitual, unidimensional, and model-free (Dolan & Dayan, 2013; Geerts et al., 2020; Poldrack & Packard, 2003; Squire, 1992). The information processing in the memory systems cooperates and competes in a sophisticated way and, as a result, underlies the behavioral expressions.

Research in computational neuroscience originates from instrumental learning studies, which stems from Tolman's cognitive maps (1948) contrasted with the stimulus-response framework by Thorndike (1898) (see Section 2.3). This computational line of research analyses the balance between two controllers of the. Reinforcement Learning (RL), known as "goal-oriented" Model-Based (MB) (hippocampal-dependent) and "habitual" Model-Free (MF) (hippocampal-independent) (Daw et al., 2005; Doya, 1999; Doya et al., 2002; Geerts et al., 2020a; Smittenaar et al., 2013b; Sutton & Barto, 2018a). In the RL, an organism is an agent confronted with a task to explore and exploit its environment in a way that allows for maximizing long-run utility. The RL framework is

usually simplified to an agent navigating states through transitions. An agent builds a tree of possible decisions (transitions) by exploring them, prunes it, and chooses an optimal action policy given a task structure and reward distribution. A proportion of activity of the MB and the MF controllers maintains a balance between exploration and exploitation. The MF controller reflects computationally efficient, automatized, and inflexible habitual behavior, while the MB controller reflects computationally expensive and flexible goal-oriented behavior (Dayan, 2009).

The information processing in the controllers simultaneously and independently influences action and decision-making (Brown et al., 2012; Brown & Stern, 2014; Ferbinteanu, 2016). Degree of cooperation and competition between the networks remains intensively investigated (Daw et al., 2011; Doll et al., 2009; Fermin et al., 2010; Gershman et al., 2012; Gläscher et al., 2010b; Otto et al., 2013; Simon & Daw, 2011; Wunderlich, Dayan, et al., 2012; Wunderlich, Smittenaar, et al., 2012). The information processed within each system can differ but still result in the same behavioral outcomes. For instance, in a T-maze, mice navigate with either place strategy (allocentric landmarks) or response strategy (egocentric turns) (Packard & McGaugh, 1996), computed respectively in RelSTR and SenSTR. Two ways of learning the same information are recognized in many fields, including instrumental learning (Dolan & Dayan, 2013; Poldrack & Packard, 2003), linguistics, where this is known as the “seesaw effect” (Ullman, 2004, 2016), or broadly speaking psychology, where memory systems are characterized as cooperating and competing (Squire, 2009b). Put simply, competition between the systems can be thought of as (over)thinking that disrupts the fluency of the currently ongoing activity.

The RL framework bears the inaccuracies of the preceding research on goal-oriented and habitual behavior (see Section 2.3). The utility function usually corresponds to the “desired rewards” from animal studies. Furthermore, for an agent to perform well, the structure of a task should have easily distinguishable states and transitions between the states, known as the Markov Decision Process (MDP) environment. In animal and human research, the MDP environment is investigated with multi-step decision tasks (Dolan and Dayan, 2013). Despite these limitations, the RL algorithms create agents capable of winning against humans in board games (Silver et al., 2018) and computer games (Vinyals et al., 2019), driving autonomously (Kiran et al., 2022), or maintaining nuclear fusion with unseen-before results (Degraeve et al., 2022).

The RL computations successfully explain and predict information processing observed in animal experiments (Geerts et al., 2020; Poldrack and Packard, 2013). The LimSTR and RelSTR closely cooperate with the HPC/EC in performing the MB computations (Poldrack & Packard, 2003), while the SenSTR underlie the MF computations (Crego et al., 2020; Daw et al., 2005; Tricomi et al., 2009). The controllers represent *opposite extremes in a trade-off between the statistically efficient use of experience and computational tractability* (Daw et al., 2005, p. 1704). The “model” refers to a mental model of the surroundings:

*Two ends of a spectrum of RL methods are model-based and model-free control (where the term model refers to a mental as opposed to a computational model); it is these that have been associated with goal-directed and habitual control, respectively (Dolan and Dayan, 2013, p.315).*

Understanding that actions span the spectrum between requiring and not requiring a mental model of the environment is understood here as the computational requirement for tracking counterfactual scenarios (the experience of the surroundings as a rich landscape of affordances). Affordances that are automated into the niche require fewer computations given that they tend to return consistent feedback and thus can be carried out as automated skills with a greater engagement of the MF controller. When the volatility of the surroundings increases, the skills are progressively open as their implementation involves anticipating the broader spectrum of counterfactual scenarios (potential futures); thus, the MB controller becomes involved. The HPC-dependent networks have been associated with computations necessary for the MB controller of the RL (Vikbladh et al., 2019). Once the MB controller designs and trains action plans, the behavior becomes exploitative and mediated by the MF controller as a sensorimotor program. The skill acquisition is reflected in a shift of computation from the MB toward the MF controller.

The RL’s research is a computational operationalization of the organism constructing its niche. Recall that ecological psychology and evolutionary biology capture the mechanism of initial exploration and subsequent exploitation as niche construction (see Section 2.3). Evolutionary speaking, the process of niche construction is understood here as exploring affordances and encoding them into memory till they can be easily retrieved as exploitative affordances. Following affordances change the

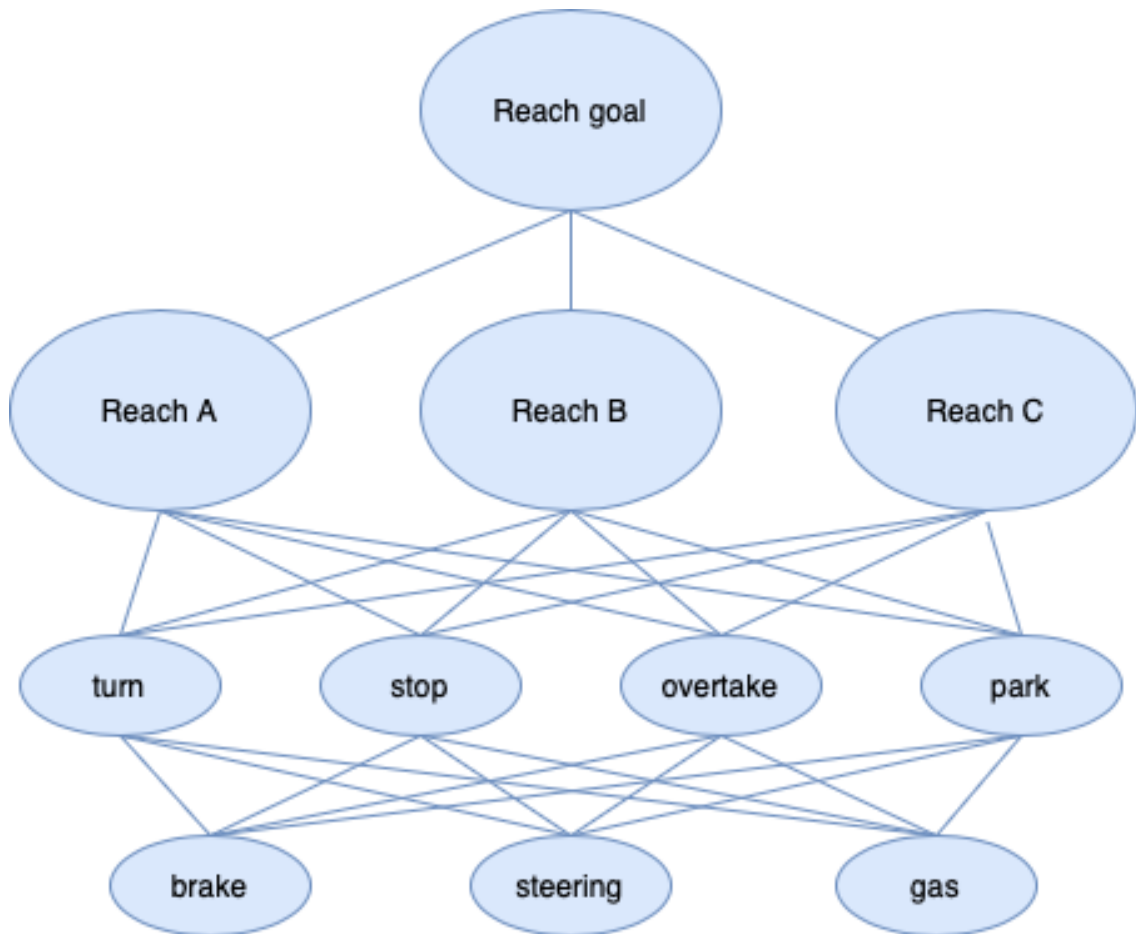
surroundings in surprising (exploration) and anticipated (exploitation) directions, which are encoded and retrieved. Niche comprises exploitative affordances computed with the MF controller; the environment consists of exploratory affordances that require the MB computation.

The information computed in the MB can be used for training the MF controller (A. Johnson & Redish, 2005; Sutton, 1991), which eventually executes habitual actions based on the cached value. The MB computations are done with learning successor representation based on the activity of the place cells in the HPC. In contrast, the MF computations are done with a learning value based on the activity of the landmark cells in the DLS (Dolan & Dayan, 2013; Ekstrom et al., 2014; Geerts et al., 2020b; Poldrack & Packard, 2003b). This implies that exploitative relations underlying a niche are embodied in the brain network processing the ongoing information flow. Similar intuition is expressed in the literature implementing the free energy principle, where the top layers of the model are believed to be “cognitive,” whereas lower layers are understood as “perceptual” (A. Clark, 2013). This is understood as a spectrum between flexibility and automaticity of the information that reaches the gestalt areas.

Organism acts in its surroundings by following affordances, balancing exploiting its niche with the MF controller and exploring its environment with the MB controller. The spectrum is gradual, and exploration eventually leads to exploitation. Exploitation is automatic, repetitive actions with known consequences that an agent retrieves from memory. When affordances are exploited, the agent repeats actions toward the familiar future state of the surroundings, anticipating that they have not changed since the last visit. On the other hand, exploratory affordances are, by definition, novel; thus, the outcomes of these actions are surprising and are learned by the agent. Based on lifelong experience, the agent encodes regularities in its surroundings, gradually shifting toward exploitation.

Crucially, dopamine is involved in both mechanisms, as this neurotransmitter mediates both encoding (Kamiński et al., 2018; Roy et al., 2022; Schultz et al., 1997; Wagatsuma et al., 2018) and retrieval (Berridge et al., 2005; da Silva et al., 2018; Frank et al., 2009; Menegas et al., 2018). Dopaminergic nuclei in the midbrain (ventral tegmental area and substantia nigra) reflect the computational gradient of the organization expressed in the striatum (Bromberg-Martin et al., 2010; McCutcheon et al., 2019, 2021) (see Sections 2.4, 6.1).

Contemporary computational research moved toward the hierarchical RL (HRL), where the time aspect of the transition between the states is recognized (Pateria et al., 2022) (**Figure 19**). The HRL decomposes the future state into a complex hierarchy of sub-states that fundamentally can be grounded in the flow of information in the sensory, somatosensory, and vestibular channels. As such, this improvement over the flat RL architecture provides a computational framework for conceptualizing the hierarchy of information processing in biological agents.

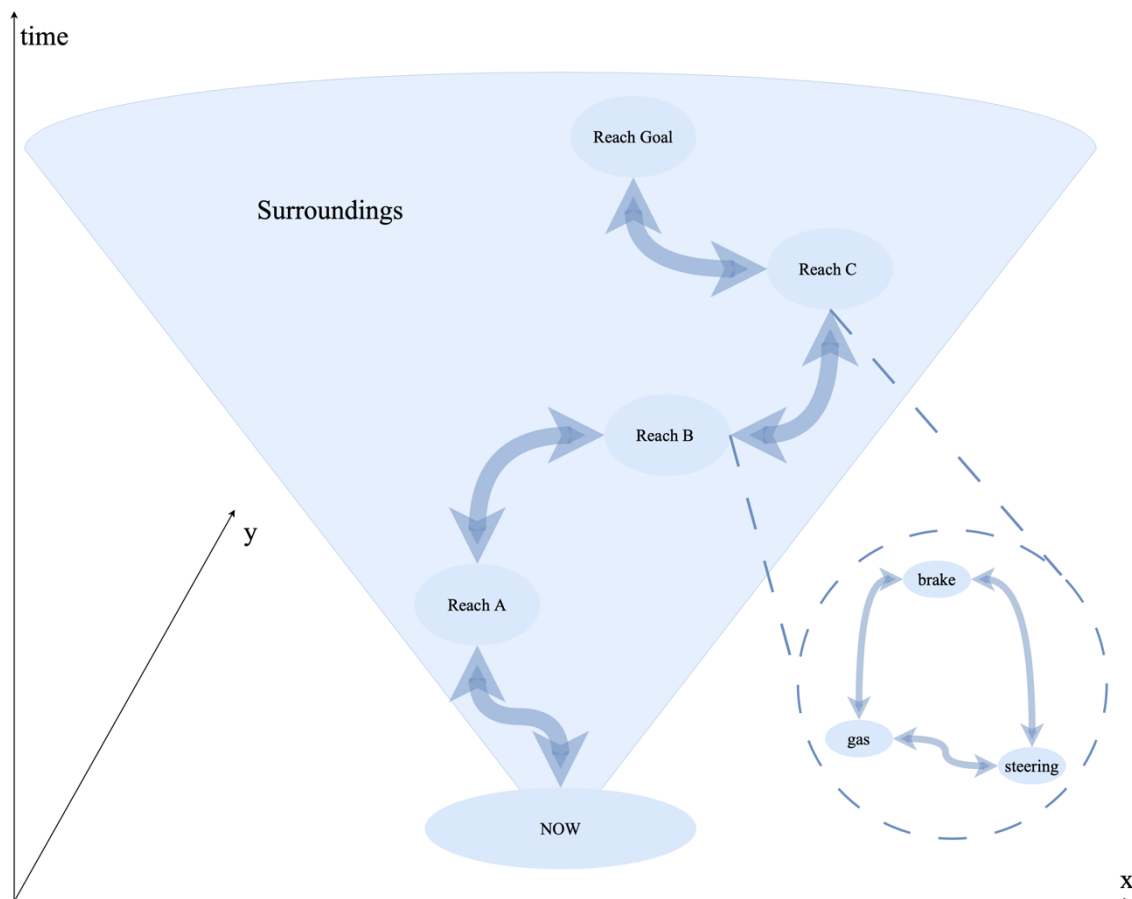


**Figure 19. Hierarchical Reinforcement Learning.** A given action can be decomposed into a hierarchy of states, sub-states, skills, and sub-skills. In the example above, the primary state (reach the destination) involves three sub-states (reach A, B, and C). The sub-states are achieved by implementing sensory, somatosensory, and vestibular information processing (skills), such as turning, overtaking, or stopping, which involve minor actions such as accelerating or steering. The sub-states are semi-Markov states that last arbitrarily long (Pateria et al., 2022). The figure is based on the example provided by Pascal Poupart during his lectures at the University of Waterloo.

The HRL algorithms evaluate the action policies when reaching an arbitrary sub-state. The action policies are arbitrarily long, and the algorithm operates beyond the MDP environment. Time spent in a given (sub)state is arbitrarily long and expressed as a semi-

Markov state where neither states nor transitions are sharp (Daw et al., 2006; Starkweather et al., 2017). Thus, semi-Markov states reflect the animal’s experience more closely than the flat architecture of the RL with the MDP environment.

Following affordances is thus implementing arbitrarily complex actions between possible futures that are hierarchically organized. Following the experienced affordances (e.g.,” reach A”) is performing sensory, somatosensory, and vestibular information processing (e.g., gas, brake, steering) (**Figure 20**). The surroundings are dynamic and reciprocal, given that transiting through/toward states opens alternative possible futures. Such understanding is also present in the free energy principle literature, where acting is inevitably tied to perceiving (Friston, 2010; Clark, 2013). Hypotheses based on free-energy minimization treat action and perception as two sides of the same coin. Action bears perceptual expectations, and perception is a prerequisite for action.

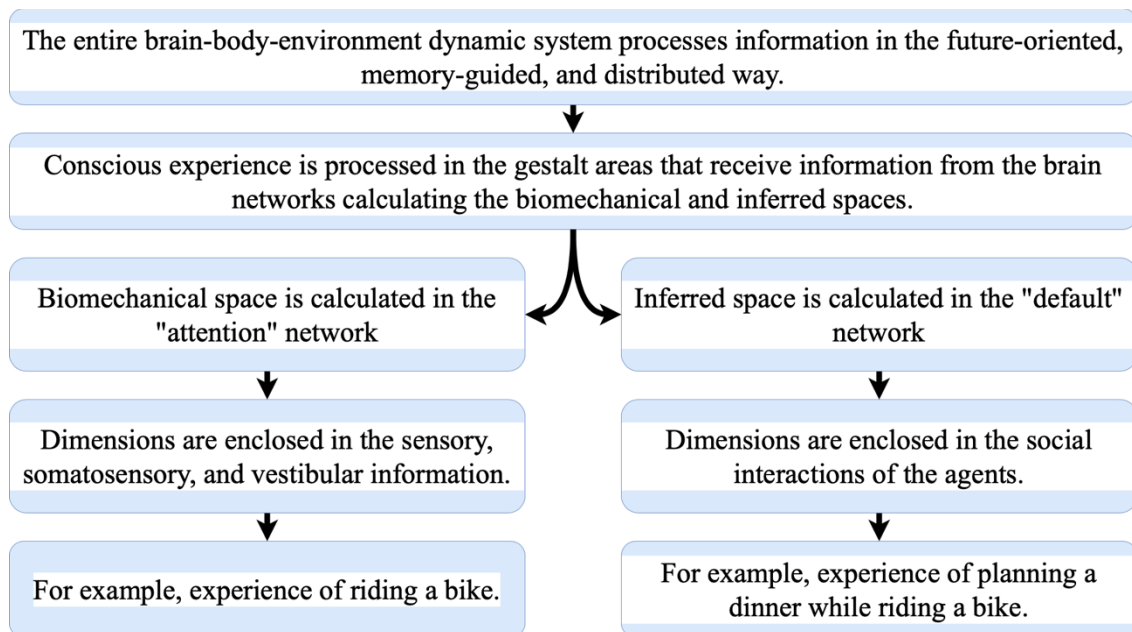


**Figure 20. Surroundings expressed in the HRL.** The surroundings are composed of the experienced potential futures that can be reached by affordances. When the affordances are implemented, they are tied to specific changes in the flow of sensory, somatosensory, and vestibular information. In the example here, the experience of reaching the subsequent sub-states is brought to the present by implementing sensory, somatosensory, and vestibular actions such as braking or steering.

## 4.5 Summary

Orientation toward the future drives learning the regularities in an animal's subjective surroundings. Distributed and future-oriented information processing system requires memory for navigating and storing the information about the statistical regularities. In a broad sense, memory underpins everything that shapes the current experience in a specific context. Memory is divided into sensory, working, and long-term memory, the last being declarative and procedural generalizations that one learned, such as conceptual knowledge or skills.

Two lines of argumentation discuss whether predicting the future is representational or ecological-enactive. Given that the information is transduced on the level of the sensorium, *everything is a representation*. Thus, here, the biomechanical space is interpreted as experience tied to processing information in the sensory, somatosensory, and vestibular channels, whereas the inferred space is interpreted as experience originating from information disconnected from these channels (**Figure 21**).



**Figure 21. The conceptual framework of information processing in action.** The entirety of information processing is distributed, future-oriented, and memory-guided. The processed information that reaches the gestalt areas is consciously experienced with the biomechanical and inferred spaces as either correlated or dissociated from the ongoing flow of sensory, somatosensory, and vestibular information.

The neurobiological structures behind the MB network are understood as computing tensors of objects and agents and their interactions regardless of the kind of surroundings (i.e., biomechanical, social). As a result of these computations,



surroundings are modeled into the hierarchical generative model of possibilities and probabilities of specific tensors. The MB computations deepen the hierarchical generative models explaining the hidden (latent) causes of the experience. Once the inferred space is encoded, the affordances between the states are trained by the unidimensional MF computations, making affordances more exploitative. If the mental model in the MB computation accurately represents the surroundings, the outcomes of the action policy are accurately anticipated, and the result is achieved without surprises. The trained affordance is “free of the model,” as the execution of the action policy relies on repeating past decisions in anticipation that the surroundings are stable and the same outcomes will be obtained. Processing of information by the two spaces representing the world takes place simultaneously and independently, which implies that the networks computing them influence each other in ontogeny and can interfere constructively or destructively.

## 5. The n-dimensional spaces of objects and agents

The previous chapter operationalized two kinds of spaces that reflect the two implementations of the free energy principle. The biomechanical spaces have been understood as the spaces where the input consists of the sensory, somatosensory, and vestibular information. The inferred spaces are the spaces that are computed with dissociation from the ongoing inputs and reflect the latent causes explaining the incoming information.

This chapter explores how the spaces are computed in large-scale brain networks. As a result of this review, the neurobiologically plausible dimensions of the inter- and intra-dimensional associations are identified as spaces computed in specific large-scale brain networks. Some spaces are calculated in the networks close to the inputs, others in the networks distant from the inputs. Once estimated, these spaces are passed to the gestalt areas, where information processing supports the conscious experience of surroundings.

## 5.1 Borders and dimensions of the spaces in the HPC-dependent network

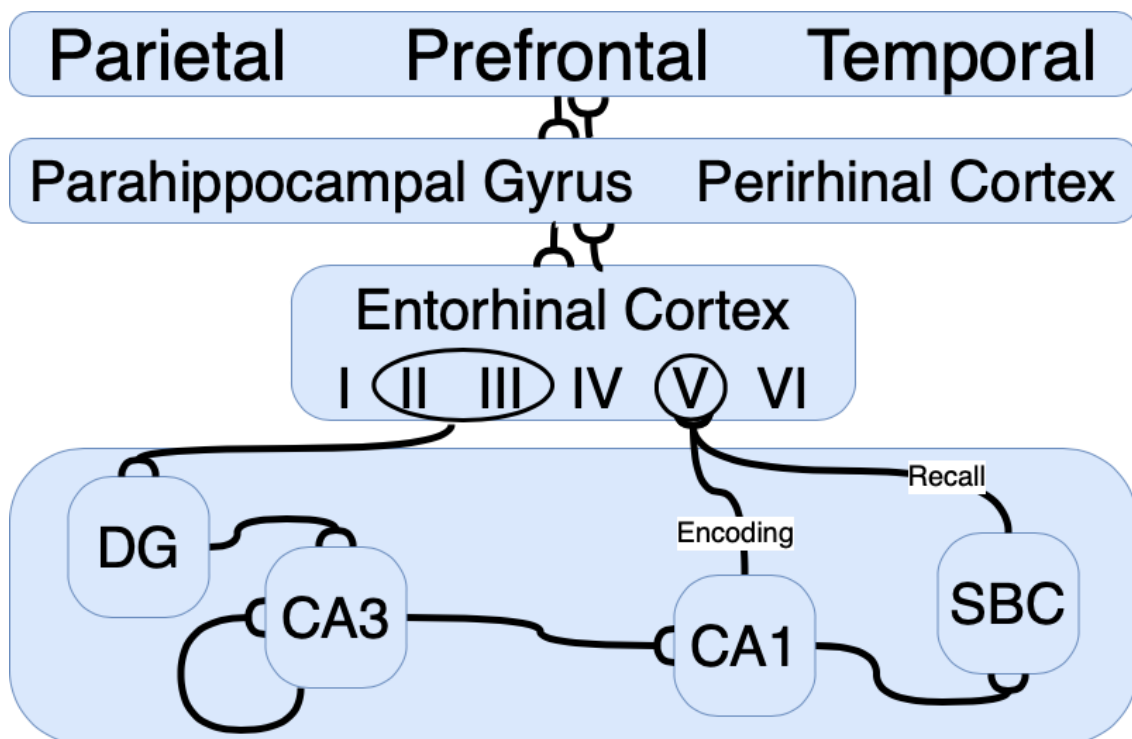
The description of space processing starts with a deepened review of the studies investigating space processing in the HPC-dependent network (see Sections 2.3, 2.4, 4.2). Recall that the HPC has been investigated for more than 60 years since the case of patient H.M. described by Squire (1992). In animal studies, Poldrack and Packard (2003) showed that rodents' flexible navigation is carried out with the HPC, LimSTR, and RelSTR, whereas the inflexible navigation with the SenSTR. Then, Dolan and Dayan (2013) showed how the research on flexible and rigid actions led to the development of computational accounts of the RL. Finally, Geerts, Chersi, Stachenfeld, and Burgess (2020) grounded the computations in the activity of specific cells in the HPC and SenSTR: the HPC computations are done with learning successor representation with the place cells, while the SenSTR computations are done with learning cached value with the landmark cells (Ekstrom et al., 2014; Geerts et al., 2020a).

The HPC-dependent computations are grounded in the information processing in the grid and place cells. The cellular components of the HPC and its connectivity are assumed to be preserved in the phylogeny, as given the neural reuse hypothesis, the biological circuitry for information processing is adapted to novel circumstances along the evolution (M. L. Anderson, 2010; Dehaene & Cohen, 2007). However, the exact information processing code in the HPC-dependent networks remains under investigation. The HPC-dependent network encloses the LimSTR and RelSTR (Poldrack & Packard, 2003) and areas in the prefrontal cortex, such as the newest evolutionary orbitofrontal cortex (Gremel & Costa, 2013; Rudebeck & Murray, 2014). Some memory researchers point toward “cognitive maps” (Behrens et al., 2018; Bellmund et al., 2020; Epstein et al., 2017; Spiers, 2020; Tolman, 1948; Whittington et al., 2022); others toward “cognitive graphs” (Ericson & Warren, 2020; Muller et al., 1996; Peer et al., 2021; Trullier & Meyer, 2000). Albeit the details are uncertain, it is universally agreed that the HPC initially evolved to navigate the physical space. It has then been reused for computing imagined navigation in abstract spaces such as social or conceptual spaces. Here, the information processing specific to the latter spaces is understood as underlying the inferred space.

The inference about the hidden causes of the incoming information is exemplified as actions performed by other agents. This claim is supported by the role of the HPC-dependent networks in computing “social space” (Danjo et al., 2018; Montagrin et al.,

2018; Tavares et al., 2015; Yeshurun et al., 2021). The HPC-dependent networks are well suited for computing objects and agents by access to the information calculated in the ventral stream that differentiates between animate and inanimate stimuli (Connolly et al., 2012; Thorat et al., 2019). These observations indicate that human cognition originates from the capacity to infer latent causes of experience as robust models of different physical and abstract agents (e.g., countries or ghosts), as the identity and abilities of the agents are inferred arbitrarily based on a posteriori evidence.

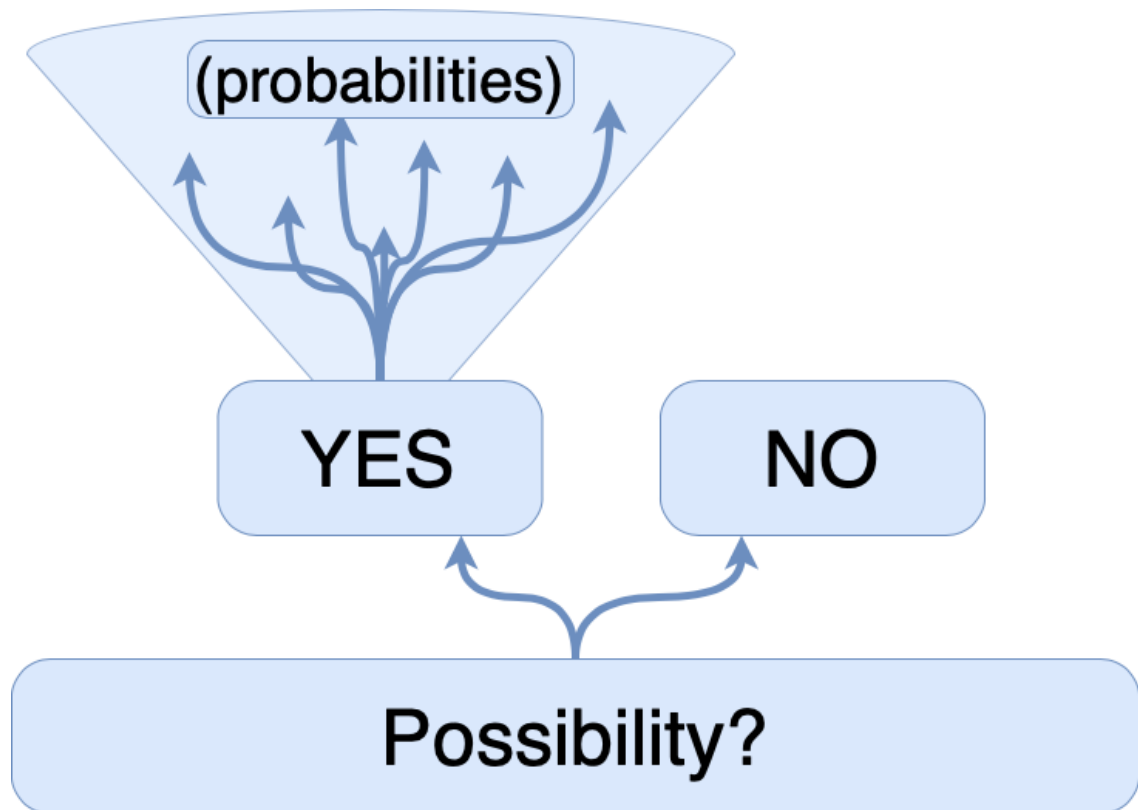
The information processing in the HPC is gated by the EC, as reflected in the TEM's computational model (see Section 4.2) (Whittington et al., 2020). The EC is the input/output structure of the HPC (**Figure 22**). The circuit through the HPC involves structurally separated and functionally organized systems within the HPC that identify the information and encode and recall parts of the engram population (Roy et al., 2022; Roy, Kitamura, et al., 2017).



**Figure 22. The simplified HPC-EC circuit.** The information flow in the HPC is gated with the EC that projects from the 2<sup>nd</sup> and 3<sup>rd</sup> layers to the dentate gyrus (DG) of the HPC. Then, the information travels along the circuit, reaching the CA1. If the information has a novel structure, it is encoded via a direct connection from the CA1 to the EC5; the known input results in memory recall and flows through the Subiculum (SBC). The 2<sup>nd</sup> and 3<sup>rd</sup> layers of the EC input information to the HPC, and the 5<sup>th</sup> layer of the EC receives the information back and subsequently propagates it. DG = Dentate Gyrus; CA3 = Cornu Ammonis 3; CA1 = Cornu Ammonis 1; SBC = Subiculum (Roy et al., 2022; Roy, Kitamura, et al., 2017).

The information processing in the HPC-dependent networks is inherently spatial for visual, conceptual, and abstract spaces. These observations prove that the computed space's structure consists of objects organized into hierarchical relations. The dimensionality of the spaces depends on objects, as the visual space is enclosed in the Cartesian coordinate system, whereas conceptual or abstract spaces may involve arbitrarily many dimensions. For example, the locomotion of rodents along a linear maze is characterized as a 1-dimensional scalar of position along the maze given time; 2-dimensional vectors describe a place on two coordinate axes. Tensors are “n-dimensional vectors” through n-dimensional spaces onto which an information processing system is distributed. The biomechanical space consists of dimensions enclosed in the sensory, somatosensory, and vestibular channels. The inferred space consists of abstract dimensions such as conceptual or social. The information processing in the HPC, understood in terms of constructing a scene, provides strong intuition that this structure is preserved across the various spaces.

Based on the information processing in the HPC-dependent network, it is claimed that the computed space is hierarchical over nested timescales and corresponds to navigation and decision-making through physical and abstract spaces. The biomechanical and inferred spaces are reduced to objects and agents exchanging information along relevant dimensions. For the biomechanical spaces, the relevant dimensions are enclosed in the sensory, somatosensory, and vestibular channels; for the inferred spaces, the dimensions emerge from the intentional states of other agents. Objects and agents travel through time along tensors concerning the possibility and probability of future interactions (**Figure 23**).



**Figure 23. Possibilities and probabilities define the spaces.** Computation of the trajectories through the spaces involves estimating the possibility of a specific trajectory and then its probability. The border cells have been identified in the EC (Solstad et al., 2008) and the SBC (Lever et al., 2009). Boundary cells have been interpreted as mediating borders in the physical and abstract spaces (Bellmund et al., 2018). Boundaries indicate that a transition in a specific direction is impossible. For the possible transitions, the studies on RL show that the HPC-dependent system is involved in the MB decision-making based on the varying probability of rewards (Feher Da Silva & Hare, 2020; Lindskog et al., 2021; Mızrak et al., 2021; Pleskac & Busemeyer, 2010). Estimating probabilities for the future is a necessary prerequisite for generating accurate predictions.

Recall that the long-term memory is procedural, i.e., consists of discrete states and transitions between these states (see Section 4.4). States are understood as circumstances that an animal generalizes as tokens of the same type (exemplars of the same category) (Gershman et al., 2010; Redish et al., 2007). For example, subsequent states reached by a delivery driver are exemplified as loading and unloading goods in specific places. The transportation between the places reflects the transition between the states. After enough repetitions, the transitions between the subsequent states become an automated skill elicited by the exploitative affordances. Thus, transitions are understood as causal links between the states conceptualized as tokens of the same type (Machery, 2009). The currently experienced state depends on the past states, which means that the agent in the past was oriented toward the future that is being experienced now. Thus,

conversely, the current state of the surroundings targets future states. In a way, orientation toward the future denotes a trajectory of causes and effects between the states in the surroundings. With memory usage, more complex surroundings can be experienced and aimed at. Understanding acting animals as agents in surroundings allows for understanding actions as changes between subsequent states of the agent's surroundings. As a result, separate classes of prediction errors related to possibility and probability are encountered, resulting in calculating other agents' potential actions. Other agents included in a given agent's surroundings can act given their intentions, desires, and beliefs; thus, an agent needs to model these intentional states for accurate predictions.

In the literature about concepts, there is a discussion about whether concepts are “modal mental representations” (Barsalou, 2008) or “amodal representations offloaded to modal brain networks” (Machery, 2016). However, discussing whether “concepts” are modal or amodal is pointless, given that psychology and philosophy operationalize the term equivocally. Instead, one shall precisely discuss exemplars, prototypes, and theories (Machery, 2009). Theories are grounded in beliefs about the causes and outcomes of a particular experience (Gopnik et al., 2004; G. L. Murphy & Medin, 1985). Thus, they are akin to the Bayesian model of the hidden causes behind the experience exemplified here as other agents. Exemplars and prototypes have been investigated in psychology for over half a century (Rosch & Mervis, 1975)), contributing to the ideas such as the “n-dimensionality” of spaces (Bellmund et al., 2018; Gärdenfors, 2004). For example, the space of colors is a three-dimensional space of hue, saturation, and lightness (Gärdenfors, 2004). Extracting relevant dimensions allows for the efficient structural organization of the information processing<sup>7</sup> (see Section 4.4).

All agents mutually try to infer accurately each others' intentional states that constitute the possibilities and probabilities in the mutual space. For example, depending on whether the parents are included in the spaces' computation, a child computes possibilities differently. Including a specific parent (or any agent, for that matter) changes the dimensions of the shared inferred space. Dimensions are parameters in the spaces.

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<sup>7</sup> The recent advancements in artificial information processing systems such as ChatGPT rely on extracting the relevant dimensions from the large data sets (Bubeck et al., 2023; Vaswani et al., 2017). It has been suggested that the HPC implements the transformer architecture in its computations (Whittington, Warren, et al., 2022). This points to an urgent research direction about the correspondence of information processing between biological and artificial systems. Understanding the dimensions of the information processing in the human's HPC might be a window for understanding both the artificial information processing.

Computations by all members of the space involve the boundaries of the space experienced as the impossibility of specific transitions. Members compute each others' actions within the accepted dimensions based on the inferred intentional states. The possibility and probability of agents' trajectories are modeled with autobiographical memory and episodic future thinking and result in assigning properties to objects and agents. Properties denote the possibilities and probabilities of transitions by other agents.

Given the above, the inferred and biomechanical spaces are computed as n-dimensional spaces filled with entities capable of various movements (executing different tensors through the shared spaces). In other words, the capacity for self-propelled motion associated with agency translates to potential transitions that other agents can implement in the shared space. For example, invasive species capitalize on the incapacity of the native species to perform specific tensors in the physical space. In the social space, dimensions such as honesty, power, and reliability are included in computing the n-dimensional space of social interactions. The possibility and probability of transitions in this space are grounded in social norms that make some tensors impossible, for example, publically wearing a specific dress at specific times. Agent breaking a social norm changes the self-distribution in the social space by modifying what is modeled as possible to do in the surroundings. This suggests that the HPC/EC computes the bordered spaces of objects and agents interacting in time according to specific rules (i.e., physical and social). The research on large-scale brain networks is reviewed in detail to investigate the neural computations behind the spaces further.



## 5.2 The spaces computed by the large-scale brain networks

So far, the information processing in the brain has been mainly operationalized in terms of the distance from the inputs. Now, the information processing in the brain is further specified by appealing to the large-scale brain networks.

The areas of the brain express varying structural and functional connectivity. Structural connectivity reflects the axonal projections between the regions. Functional connectivity denotes how areas are coupled in specific experimental settings. For example, perceiving an image result in activation in the early visual cortices, then the information flows along the ventral stream (the LOCT, the VTC) that contributes to the conscious experience and reaches the HPC-dependent network for memory encoding (see Section 3.2).

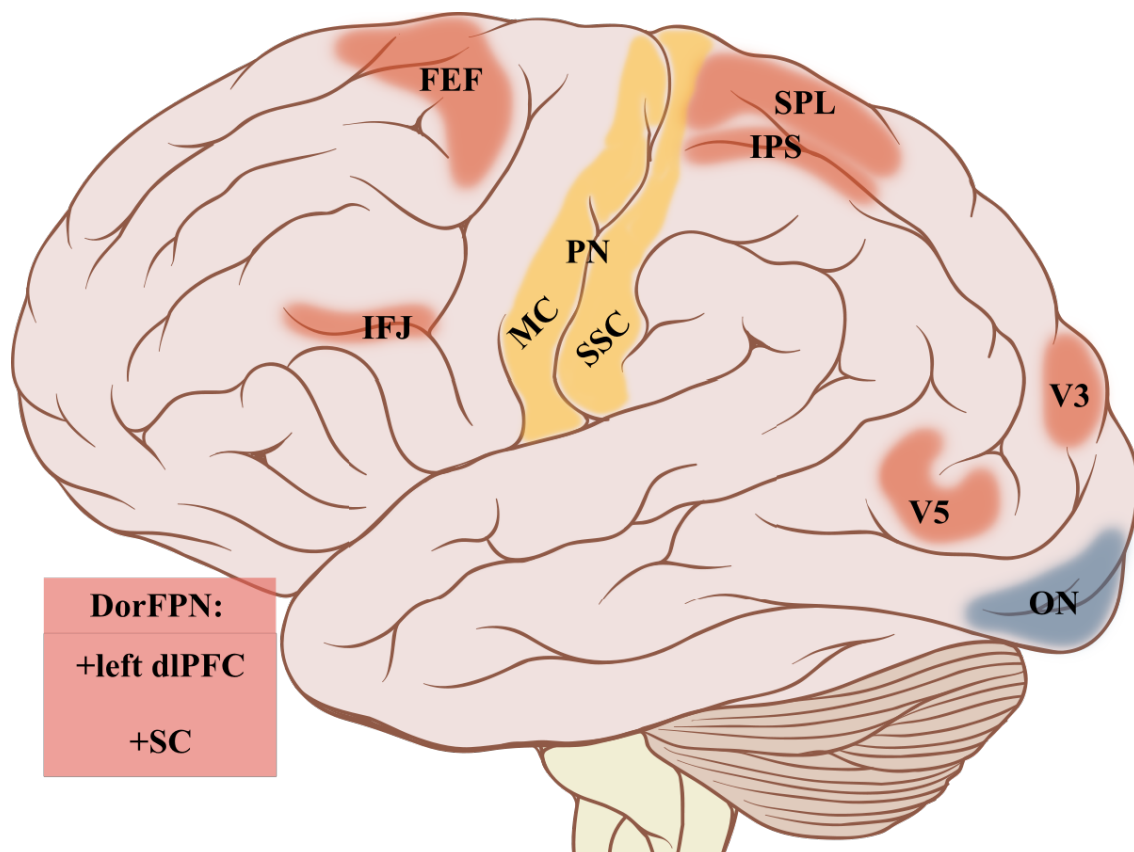
The last ten years brought much progress in identifying large-scale brain networks implementing functionally distinct information processing. Studies use brain imaging to determine the structural and functional coupling between the brain areas, thus pointing out the taxonomy of large-scale brain networks. However, the rapid accumulation of such studies results in inconsistent terminology and uncertainty about the number and composition of large-scale brain networks. Here, the taxonomy differentiating the six large-scale brain networks is adopted (Uddin et al., 2019) (**Table 2**).

<b>Short</b>	<b>Name</b>	<b>Roles</b>
<b>ON</b>	Occipital Network (visual)	Process early visual information
<b>PN</b>	Pericentral Network (somatomotor)	Process somatosensory and motor information, connects with SenSTR.
<b>MidCIN</b>	Midcingulo-Insular Network ( <b>salience</b> )	Process emotional (salient) and rapidly allocates attentional processes toward them.
<b>DorFPN</b>	Dorsal Frontoparietal Network ( <b>attention</b> )	Prepare and apply top-down visuospatial attention.
<b>LatFPN</b>	Lateral Frontoparietal Network ( <b>control</b> )	Goal-oriented cognition, working memory, inhibition and task switching, connects with RelSTR
<b>MedFPN</b>	Medial Frontoparietal Network ( <b>default</b> )	Reconfigure associative representations, plan, engage in goal-directed tasks, imagine, reflect, theory of mind, reason counterfactually.

**Table 2. Universal taxonomy of large-scale human brain networks.** The Pericentral Network (PN) processes information from the primary motor and somatosensory cortices. The Occipital Network (ON)

consists of the early visual areas and processes the visual information. The dorsal FrontoParietal Network (DorFPN) processes visuospatial attention. The lateral FrontoParietal Network (LatFPN) involves executive functions such as goal-oriented cognition, working memory, inhibition, and task switching. The medial FrontoParietal Network (MedFPN) is also known as the “default mode network” and is involved in reconfiguring associative representations, imagination, and Theory of Mind. The midCingulo-Insular Network (midCIN) is also known as the “salience network.” It is responsible for rapidly switching attention toward behaviorally salient stimuli, such as threats, both experienced and remembered. The brain areas enclosed in the networks remain discussed, as depending on the task, different regions become synchronized—for example, the LatFPN couples with the DorFPN or the MidFPN in stimulus-driven or internally-directed tasks (Dixon et al., 2018). Based on Uddin (et al., 2019).

The ongoing flow of sensory, somatosensory, and vestibular information is predominantly processed by the ON and PN (**Figure 24**) (Gordon et al., 2017; Yeo et al., 2011). The ON processes early visual information into the ventral and dorsal streams (see Section 3.2). The PN is involved in processing primary motor and somatosensory information. Recall that the PN and ON project to associative brain areas computing the peri-spaces, such as the IPS (see Section 1.2), which is included in the DorFPN.



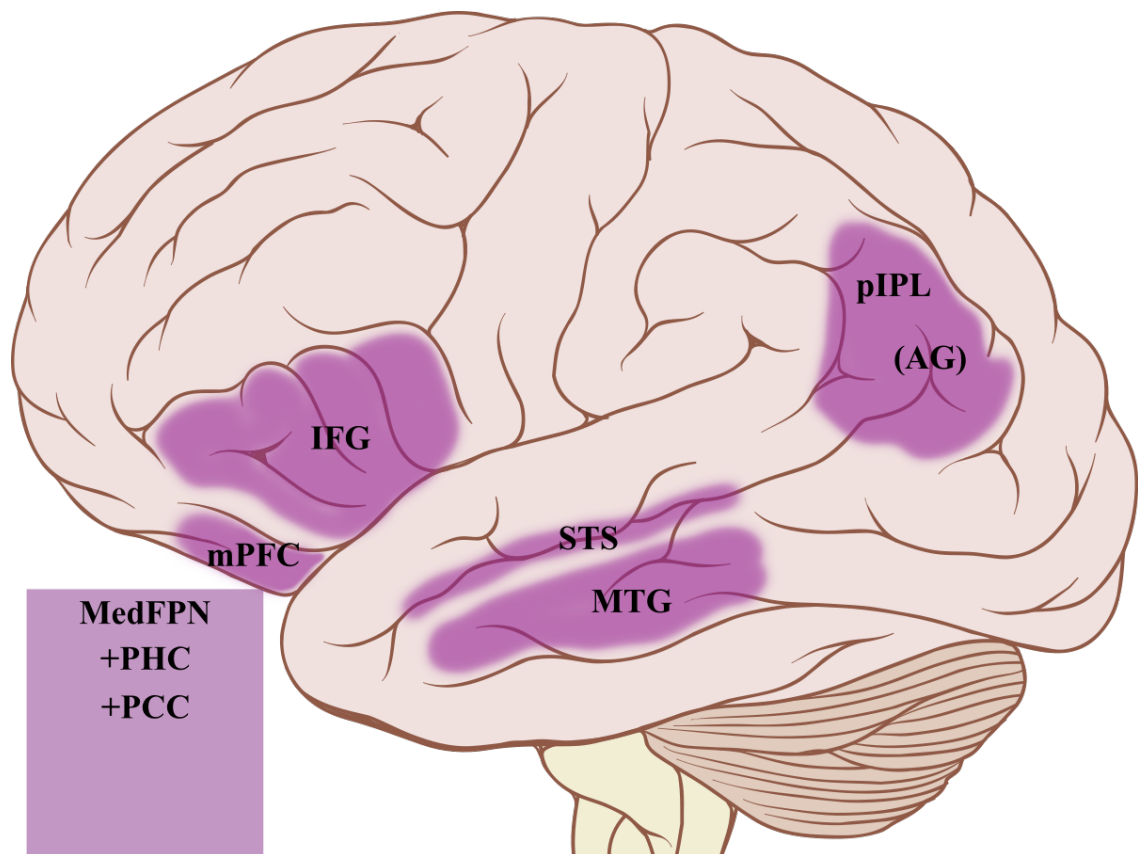
**Figure 24. The networks that process the incoming information.** The pericentral network (PN) processes somatosensory and proprioceptive information, and the visual network (VN) processes visual input (Gordon et al., 2017; Yeo et al., 2011). Note that the PN process information from the motor and somatosensory cortices, while the ON process visual information and constitutes an origin for the ventral

and dorsal streams of visual processing (Milner, 2017). The dorsal frontoparietal network (DorFPN) is involved in spatiotemporal visual attention as it encloses associative areas computing the peri-spaces (Maravita & Iriki, 2004; Serino, 2019) and areas calculating eye movements, such as the frontal eye field (FEF) and superior colliculus (SC). The figure presents a taxonomy suggested by Uddin (et al., 2019). DorFPN = Dorsal FrontoParietal Network, dlPFC = dorsolateral Prefrontal Cortex, SC = Superior Colliculus, IFJ = Inferior Frontal Junction, FEF = Frontal Eye Field, SPL = Superior Parietal Lobule, IPS = Intraparietal Sulbus, V3 and V5 = visual areas; PN = Pericentral Network, MC = Motor Cortex, SSC = Somatosensory Cortex; ON = Occipital Network.

The DorFPN, also called the attention network, prepares and applies selection for stimuli and responses (Corbetta & Shulman, 2002; Rueda et al., 2004). Thus, this network mediates top-down attention, in contrast to the bottom-up attention endogenously generated by the “salience” MidCIN (Goulden et al., 2014; Uddin, 2016). The areas included in the DorFPN suggest that this network coordinates the flow of visual and somatosensory information in the human brain.

Conversely, the information dissociated from the incoming inputs is processed by the MedFPN, also called “the default mode network” in the literature (Uddin et al., 2019). Initially, this network was identified in resting state activity when participants undergoing brain scans were disengaged from tasks (Raichle et al., 2001), hence the name “default” pointing to the baseline activity of the brain. Subsequent investigations revealed that the network consists of functionally separated subnetworks (C. Murphy et al., 2018; Uddin et al., 2019) that can contribute to performance in the ongoing tasks (Beaty et al., 2015; Crittenden et al., 2015; Sormaz et al., 2018). The MedFPN is defined in the literature as “the most distant from input” brain network (Murphy et al., 2018).

The organization of the MedFPN satisfies the criteria for computing the inferred spaces, which has been suggested in the literature (Carhart-Harris & Friston, 2010; Dohmatob et al., 2017). However, the exact details of this brain network remain mysterious, given that the network is involved in a broad spectrum of seemingly unconnected functions. Here, the MedFPN is grounded in a broader context of information processing in the brain by identifying the core areas included in the MedFPN reviewed by Uddin and colleagues (2019) (**Figure 25**).

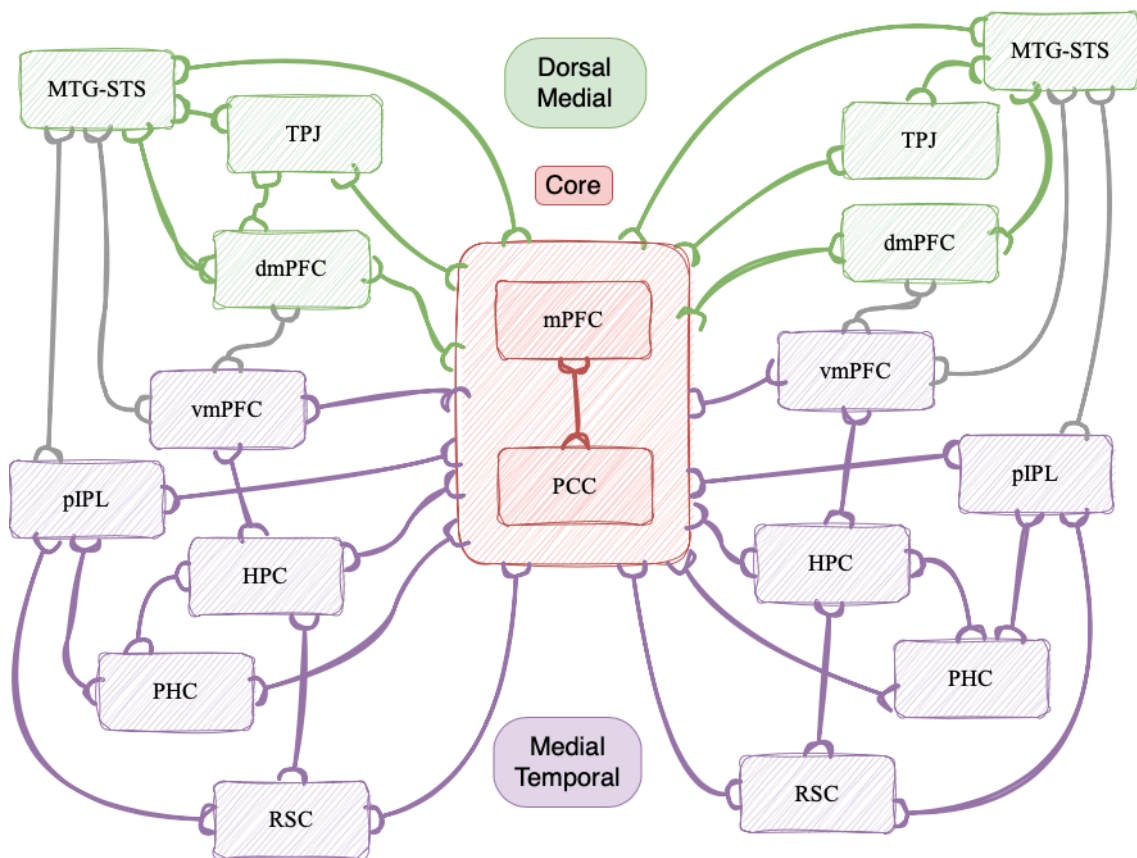


**Figure 25. The medial frontoparietal network.** The network, also known as the default mode network, is operationalized as the brain network processing information most distant from the inputs (C. Murphy et al., 2018). According to the review by Uddin (et al., 2019). The core areas included in the MedFPN are (I) the medial Prefrontal Cortex (mPFC), which location extends medially from the area depicted in the figure. This area associates a broad range of information (P. Xu et al., 2019) and is considered a central hub of the MedFPN (Uddin et al., 2019). (II) The inferior frontal gyrus (IFG), which corresponds to Broka’s area, produces sequences of actions in detailed resolution, such as language (Ullman, 2006). (III) The superior temporal sulcus (STS) is involved in detecting and understanding intentional actions (Hein & Knight, 2008; Shultz et al., 2011). (IV) The middle temporal gyrus (MTG) is involved in semantic processing (Wei et al., 2012), specifically in integrating conceptual information from the temporal pole (Landi et al., 2021) with potential actions (J. Davey et al., 2016). (V) The posterior inferior parietal lobule (pIPL) with the angular gyrus (AG) is involved in computing action and perception (Niu et al., 2021) , and this region is highly developed in humans (Igelström & Graziano, 2017). Areas not shown in the figure include (VI) the parahippocampal cortex (PHC) that computes contextual associations (Aminoff et al., 2013) and (VII) the posterior cingulate cortex (PCC), which is located approximately in the center of the brain, is one of the main hubs of the MedFPN and is involved in broadly understood “internally-directed cognition” (Leech & Sharp, 2014). mPFC = medial prefrontal cortex; IFG = inferior frontal gyrus; STS = superior temporal sulcus; MTG = middle temporal gyrus; pIPL = posterior inferior parietal lobule; AG = angular gyrus; PHC = parahippocampal cortex; PCC = posterior cingulate cortex.

The reviewed functions of the components of the MedFPN indicate that this network is involved in processing abstract associations between abstract information. To investigate these computations further, the subdivisions of the MedFPN are analyzed.

The MedFPN can be decomposed into a core network that constitutes a communication hub and two subnetworks: (I) medial temporal and (II) dorsal medial (**Figure 26**). The core network specializes in self-processing, the subnetworks in mind-wandering and mentalizing (Uddin et al., 2019)<sup>8</sup>

Organization of the Medial Fronto-Parietal Network in primates:



**Figure 26. Organization of the MedFPN.** The network is divided into three subnetworks associated with self-referential processes (red), imagination (violet), and attributing mental states to others (green). (based on Andrews-Hanna et al., 2010; 2014; Uddin et al., 2019).

Note that the medial temporal subnetwork areas overlap with the HPC-dependent network discussed in the previous chapters (see Sections 2.3, 2.4, 4.2, 5.1). This network has been called a “generic recollection network” (Hayama et al., 2012; Schacter et al., 2012) as its functional role involves imagination and memory recall. Essentially, these

<sup>8</sup> Note that Uddin (et al., 2019) include the mPFC and PCC into the medial temporal subsystem. They differentiate two subnetworks, not three as in Andrews-Hanna (et al., 2010; 2014).

observations point out that the scene computations in the HPC (Maguire et al., 2016; Maguire & Mullally, 2013) apply to the entire medial temporal subnetwork.

The **dorsal medial subnetwork** is characterized in the literature as the mentalizing network involved in the inference of mental states of other agents (Spunt & Lieberman, 2012; Van Overwalle & Baetens, 2009). According to Andrews-Hanna (et al., 2010), this network consists of dmPFC, TPJ, and MTG-STT (called there the lateral temporal cortex - LTC). The areas suggested above differ from those included in MedFPN by Uddin and colleagues (2019). Their other study reviewed research on self-related cognition that points to the mirror neuron system composed of the “*inferior frontal cortex*” and “*rostral part of the inferior parietal lobule*” (Uddin et al., 2007 Box.2), which later are labeled as IFG and aIPL and are included in the MedFPN (Uddin et al., 2019). However, as shown in Andrews-Hanna (et al., 2014, p. 31), the IFC (Broka area) is active only in the resting state, while in functional imaging, the activation of the IFC is missing. This possibly implies that IFC’s activity in rest corresponds to internal dialogue. Nevertheless, such observation points out the importance of time and context in which the networks are investigated.

The **core network** is composed of the mPFC and PCC (Andrews-Hanna et al., 2010, 2014; Uddin et al., 2019). These two areas are central hubs of the MedFPN, expressing the most robust connectivity with the remaining parts of the network. Some studies suggest that in addition to the mentioned structures, the core regions are also the pIPL, MTG, STS, and SFG (Yeo et al., 2011). However, these regions are not counted in the core regions of the MedFPN in subsequent articles (Andrews-Hanna et al., 2014; Uddin et al., 2019).

The MedFPN remains to be operationalized more precisely as the available literature differs in the adopted taxonomies and terminologies. This issue, albeit addressed by Uddin and colleagues (2019), still needs to be solved. Therefore, in the remaining part of this review, the MedFPN is analyzed broadly as the core network and two subnetworks combined. Additional research on imagination and the evolutionary roots of social processing are reviewed.

The MedFPN is associated with future imagination (Bellana et al., 2017) and imagery vividness (Lee et al., 2021). The imagery of specific situations may resemble actual experiences to the extent that fear of extinction (Reddan et al., 2018) or muscle growth (Ranganathan et al., 2004) is observed in the imagining participants. The MedFPN is crucial for imagination, an experience of sensory, somatosensory, and

vestibular information disconnected from the ongoing inputs (C. Murphy et al., 2018). This operationalization makes the imagination content unbounded and distributed along the exploration-exploitation spectrum, as in the already mentioned example of the memory palace (Mecacci, 2013). Research on imagination focuses mainly on visual imagination, where a range between *incapacity* to imagine visually (aphantasia) (Fulford et al., 2018; Milton et al., 2021) and experience of the combination of senses (synesthesia) to real-like vividness of imagined scenes (Mecacci, 2013) have been identified. Imagination is broadly divided into four kinds associated with the MedFPN: dreaming, mind-wandering, autobiographical narratives, and counterfactual thinking (Carroll, 2020). This paragraph points out that imagination is idiosyncratic, and its neural correlates span the HPC-dependent network and the MedFPN.

In some studies, the mPFC is labeled the orbitofrontal cortex (OFC), which is the most evolutionary recent structure of the brain that performs sophisticated information processing (Daw et al., 2006; Valentin et al., 2007). The OFC balances the activity between the parts of the striatum (Gremel & Costa, 2013) (see Section 2.4). The functional organization of the OFC is believed to reflect the computations on the mental model that the MB controller is involved in (Rudebeck & Murray, 2014) (see Section 4.4). The anterior part of the OFC represents the stimulus associated with the outcome (e.g., candy packaging), the posterior part signals the sensory qualities of the specific effect (e.g., the taste of a candy), and the lateral portion correlates with computing choices, the medial portion signals the consequences of an option which an animal is about to make (Rudebeck & Murray, 2014). However, the role of the OFC is even more elusive, given that without the OFC, an animal can still learn, relearn, and replace associations, although more slowly than its healthy counterparts (Wilson, Takahashi, et al., 2014). This kind of information processing involving perceptually inaccessible information is also known as cognitive control (Badre, 2008). Thus, the suggested function of the OFC is to recognize the perceptually similar states that differ regarding some perceptually non-available features (Wilson, Takahashi, et al., 2014), which reflects a mental model of the surroundings expressed as time trajectories of objects and agents onto which an information processing system is distributed.

Additionally, the MedFPN in *H. Sapiens* is differently organized than in the other primates (Garin et al., 2022). In all primates except humans and chimpanzees, the core regions of the MedFPN (mPFC and PCC) are not connected, which explains how chimpanzees can understand psychological states (Tomasello et al., 2003). The MedFPN

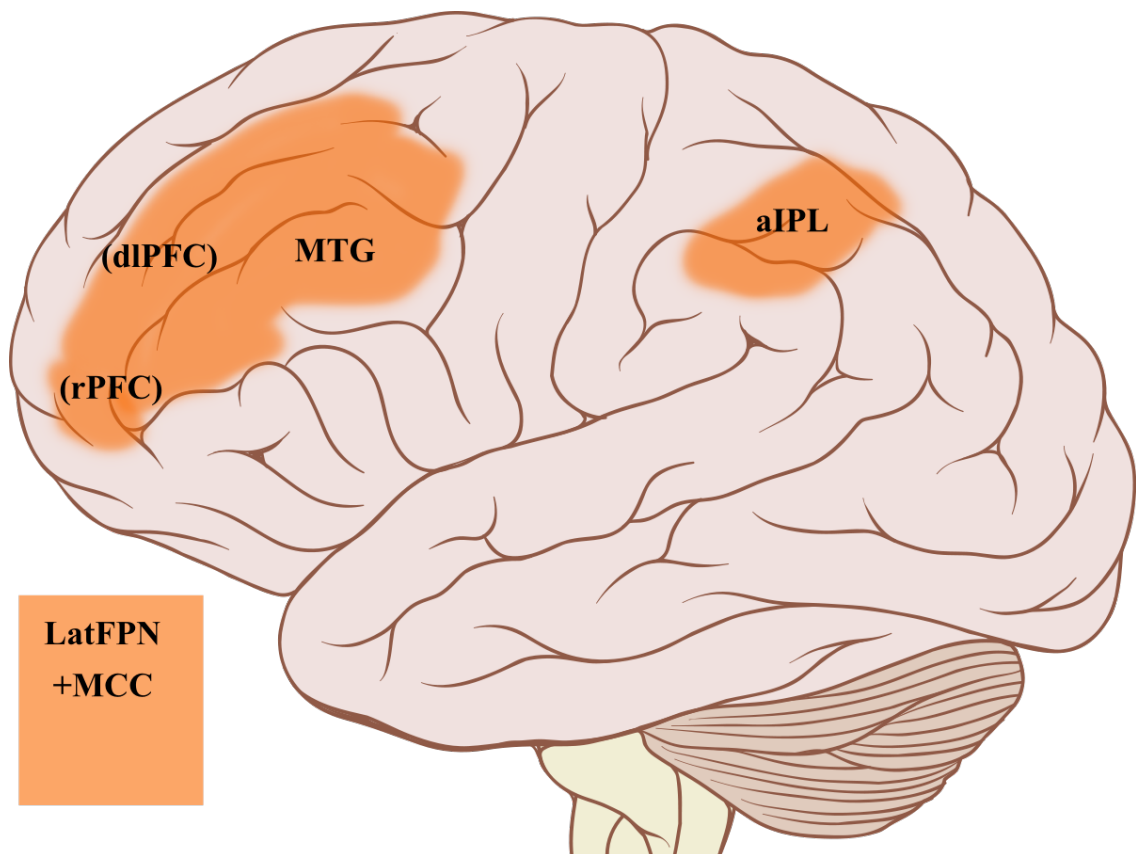
is involved in broadly understood social information processing (Buckner & Carroll, 2007; C. G. Davey et al., 2016; Li et al., 2014; Spreng et al., 2009; Wang et al., 2021; Yeshurun et al., 2021). The phylogenic development of the core subnetwork of the MedFPN appears to support the evolutionary arguments that the capacity to establish joint attention has driven human evolution (Tomasello, 2010, 2019; Tomasello & Rakoczy, 2003).

Taken together, the MedFPN is decoupled from experience (C. Murphy et al., 2018; M. Zhang et al., 2022). It contributes to information processing in multiple functional systems during action execution (Mancuso et al., 2022; Tong et al., 2022). Contrary to initial findings (Raichle et al., 2001), the MedFPN is *not* negatively correlated with performing tasks and is involved in numerous executive functions (Cole et al., 2014; Sormaz et al., 2018; Spreng et al., 2010; Vatansever et al., 2015). Therefore, the MedFPN is understood as computing the inferred spaces that contribute to the conscious experience of surroundings for the sake of actions.

The activity of the “attention” DorFPN and the “default” MedFPN may seem anticorrelated as the former network computes biomechanical space grounded in the incoming information, while the latter computes the inferred space distant from inputs. However, studies show that during ontogeny, the MedFPN trains the immature DorFPN (M. Chen et al., 2022), and the networks are increasingly less anticorrelated in older adults (Spreng et al., 2016). This is understood as a neural manifestation of adulthood, i.e., commitments to specific life aspects that are no longer counterfactually considered. Nevertheless, the volatile surroundings experienced by acting organisms involve uncertainties that must be resolved. The role of adjusting the information flow between the networks depending on the task’s demands is served by a third network – the LatFPN.

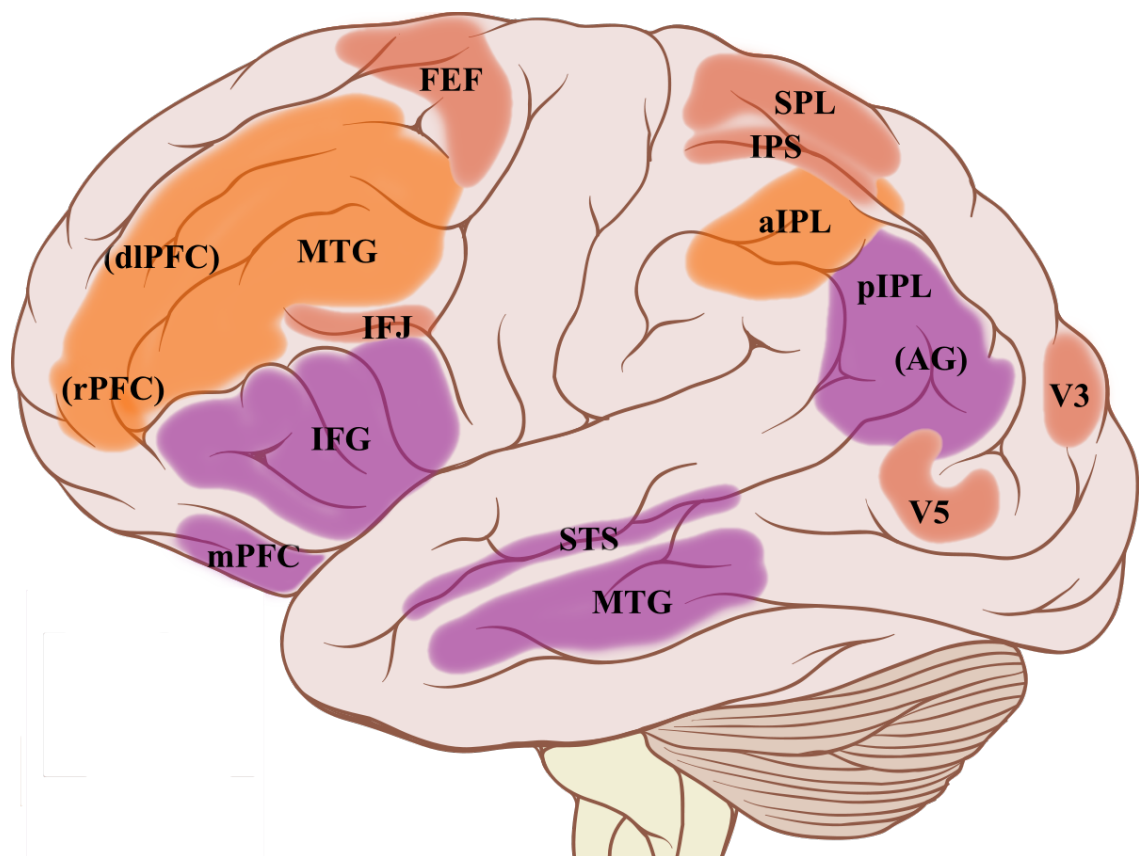
The LatFPN is also called a control network, given its broad role in the executive and goal-directed control of the information flow (Smith et al., 2009; Uddin et al., 2019) (**Figure 27**). This network is involved in working memory, inhibition, task switching, and goal-oriented actions.





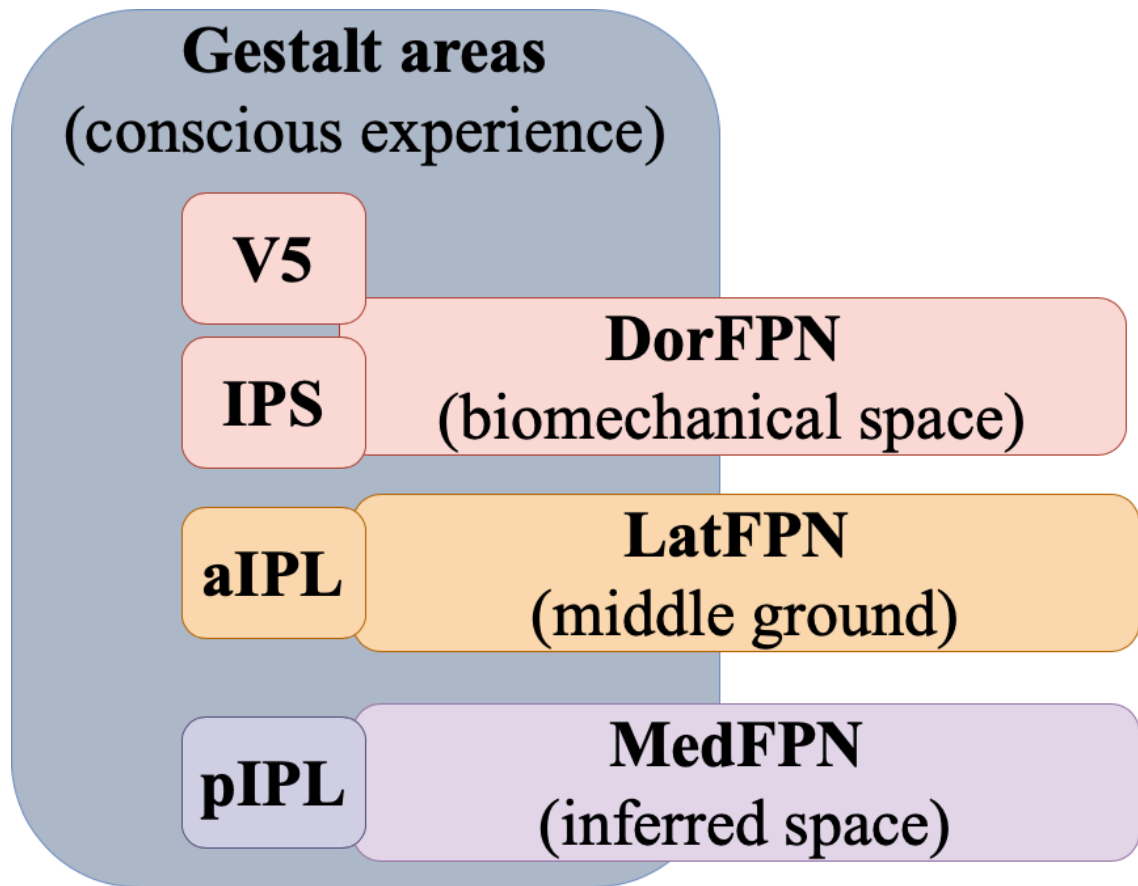
**Figure 27. The lateral frontoparietal network (LatFPN).** This network is also called a control network associated with executive control (Smith et al., 2009; Uddin et al., 2019). LatFPN = Lateral FrontoParietal Network; MCC = Middle Cingulate Cortex, dPrecuneus = dorsal Precuneus, dmThalamus = dorsomedial Thalamus, RelSTR = Relational Striatum (head of caudate nucleus), MFG = Middle Frontal Gyrus, aIPL = anterior Inferior Parietal Lobule, ITC = Inferior Temporal Cortex.

The areas included in the LatFPN are also labeled as the multiple-demand network (Duncan, 2010) associated with intelligence (Duncan et al., 2020). Other names are the cognitive control network (Niendam et al., 2012), the frontoparietal control network (Dosenbach et al., 2008; Vincent et al., 2008), the domain-general system (Fedorenko et al., 2013), and the central executive network (Seeley et al., 2007). Functional connectivity of information processing in the LatFPN predicts the performance in complex tasks such as playing demanding games (Chenot et al., 2021). The information processing in this network is coupled with the DorFPN and MedFPN, depending on the task's demands (Dixon et al., 2018), which points to the role of this network in balancing the activity of the MedFPN and DorFPN (**Figure 28**).



**Figure 28.** The areas included in the three networks. The core areas of the DorFPN (red), MedFPN (violed), and Lat FPN (orange) are suggested by Uddin and colleagues (2019). Notice how areas from all three networks overlap with gestalt areas, specifically the IPS, aIPL, pIPL with AG, and V5.

The information processing in the large-scale brain networks encloses “non-representational” information received by the receptors and “representational” information processed within the specialized brain networks. The information computed in the ON and PN are as “non-representational” as possible, given that these networks correspond to primary sensory areas. The information in the DorFPN is organized into biomechanical space; thus, its format is interpreted as “representational”. Similarly, the MedFPN is a “representational” network because it computes the inferred space. The LatFPN balances the activity between the DorFPN and MedFPN depending on the following affordances and incoming information. All three networks contain regions classified into gestalt areas (**Figure 29**). Specifying their role is, however, beyond the scope of this article. Instead, the focus is on identifying the structure of the inferred space computed in the MedFPN by reviewing the research on the Theory of Mind.



**Figure 29. Neural computations behind the framework.** Gestalt areas mediate the conscious, effortless, and pre-reflective experience of the subjective construal (Lieberman, 2022). Experience of the construal for the sake of action is an experience of the surroundings understood as the rich, hierarchical landscape of affordances organized from exploitative (niche) to explorative (environment). The three large-scale brain networks contain the regions included in the gestalt areas.

### 5.3 The inferred space is investigated in the Theory of Mind (ToM)

The surroundings computed with the inferred space involve information processing dissociated from the flows of sensory, somatosensory, and vestibular information; thus, it is claimed that this information is computed in the MedFPN as n-dimensional space of latent causes, exemplified as actions of other agents. When the information reaches the gestalt areas, it is consciously experienced as agents with intentional states (desires, intentions, and beliefs) that affect their potential movements. This understanding is hardly used in computational neuroscience as research on instrumental conditioning focuses on “desirable” outcomes (Dolan & Dayan, 2013), initially developed in animal research and directly adapted to research on humans (Dickinson, 1994; Dolan & Dayan, 2013). It happened without the interdisciplinary collaboration with philosophers, who have been arguing for the complexity of intentional human states (Bratman, 1991; Mele, 1992; Pacherie, 2008; Searle, 1983), which originate from the richness of possible causes and reasons for actions (Davidson, 1963). The complexity of intentional states in *H. Sapiens* makes direct translation of *desirable states* from the rodent literature inappropriate. The processes behind the inference of other agents’ intentions, desires, and beliefs are omitted in the research on instrumental learning. They are, however, recognized in psychological research on the Theory of Mind (ToM).

The research on the ToM points to an inference of intentional states of other agents as factors determining the modeled possibility and probability of agent’s movements in the social space. Agents interact predictably/surprisingly and create complicated relations such as symbiotic (parasitism – commensalism – mutualism) or predator-prey (Bousquet & Le Page, 2004; Farmer & Foley, 2009). Thus, the experience of the surroundings involves recognizing entities with agency (which correlates with the capacity for self-propelled motion). The perceived agency is understood as the factor differentiating between processing an identity of certain information in the VTC as animate agents and inanimate objects. This implies that the characteristics of the self-propelled movement of the experienced agents should also be processed, such as their inertia and acceleration. Thus, the information processing behind the inferred space necessarily entails modeling other agents’ capacities to move according to the possibility and probability of these movements. Multiple agents process information simultaneously, mutually modeling themselves as parts of their surroundings that must or mustn’t be reckoned with.

The ToM investigates how agents acquire beliefs about the intentional states of other agents (Frith & Frith, 2006; H. L. Gallagher & Frith, 2003; Goel et al., 1995). In developmental psychology, children's ToM is usually tested with a scene of two dolls that differ in knowledge about the location of an item – a test known as the Sally-Anne test (Baron-Cohen et al., 1985; Korziakangas et al., 2016). To pass a test, a child has to adopt the perspective of a particular doll, which reflects inference about its beliefs.

The inference of intentional states of other agents is also investigated in sociological research on children and primates, particularly by Tomasello (2009). Tomasello argues that the ability to create shared intentions is the basis for modern human culture. In studies of toddlers, Tomasello found that children as young as nine months old can establish and maintain joint intentions when playing with their caregivers. Children develop collective intentionality by the age of three. Collaboration among humans is unique due to our ability to establish mutual understanding toward a common goal (Tomasello, 2009). Chimpanzees work together but do so competitively, without fairness between individuals (Tomasello, 2019). Humans can establish a joint goal and regulate the behavior of others involved through normative statements that reflect the possibility and probability in the computed spaces. According to Tomasello, humans can self-regulate through a sense of obligation, which corresponds to establishing borders of space by normative statements. These findings are interpreted here as an experience of a potential future mutually shared between the involved agents. It means each participating agent experiences affordances that require the remaining agents to act.

The studies on the ToM point out that humans can establish potential futures in shared surroundings. Contrary to other aspects of distributed information processing among animals, this capacity for collective action is kept from other primates. Humans are unique in their ability to process information socially and work together to achieve joint goals. The surroundings are experienced, given the inferences about the intentional states of other agents in the multiagent agent's surroundings. Once surroundings are mutually shared, all involved agents can follow the affordances toward the potential futures, and along the subsequent repetitions, they become exploitative. For example, interactions during grocery shopping or traffic are exploitative affordances with culturally shared anticipations. Such actions are known as deontic actions (Constant et al., 2019). In other words, these actions are ontologically acquired skills. Involved agents accurately model their mutual trajectories in the inferred space. In such cases, every agent accurately retrieves beliefs about the causes and effects of the shared surroundings.

The surroundings computed from the inferred space consist of potential interactions of the agents, including the organism itself. This builds on the notion of experiencing and remembering self (Kahneman and Rills, 2005; Zajchowski et al., 2017). The experiencing self experiences the flow of sensory, somatosensory, and vestibular information computed in the DorFPN; the remembering self experiences the memory dissociated from the ongoing flow, presumably calculated in the MedFPN. The remembering self computed in the inferred space is investigated in psychology as the episodic memory related to one's past, known as autobiographical memory (Tulving, 2002). The capacity for remembering autobiographical memories differs between individuals (LePort et al., 2012; Palombo et al., 2015, 2018; Watkins, 2018). Autobiographical memory reflects the remembering self, given that it captures what a specific individual considers himself to be. It is here recognized that one frames oneself into the model of intentional states, similarly to other agents into models of their intentional states<sup>9</sup>. In essence, the agent's beliefs about hidden causes and effects translate to models of the agent and other agents in the computed spaces<sup>10</sup>.

One needs to note that agents infer models of other agents as causes and effects of actions in a biased way, ultimately leading to naïve realism (Lieberman, 2022; Ross & Ward, 1996). The surroundings are inferred with a subjective bias, albeit to a certain depth of computation; these surroundings are intersubjective (aligned) within a particular class of individuals. For example, terms such as “neurotransmitters,” “money,” or “Zeus” are intersubjective insofar as the groups of individuals, such as a research group or a tribe, infer it intersubjectively as hidden causes and effects.

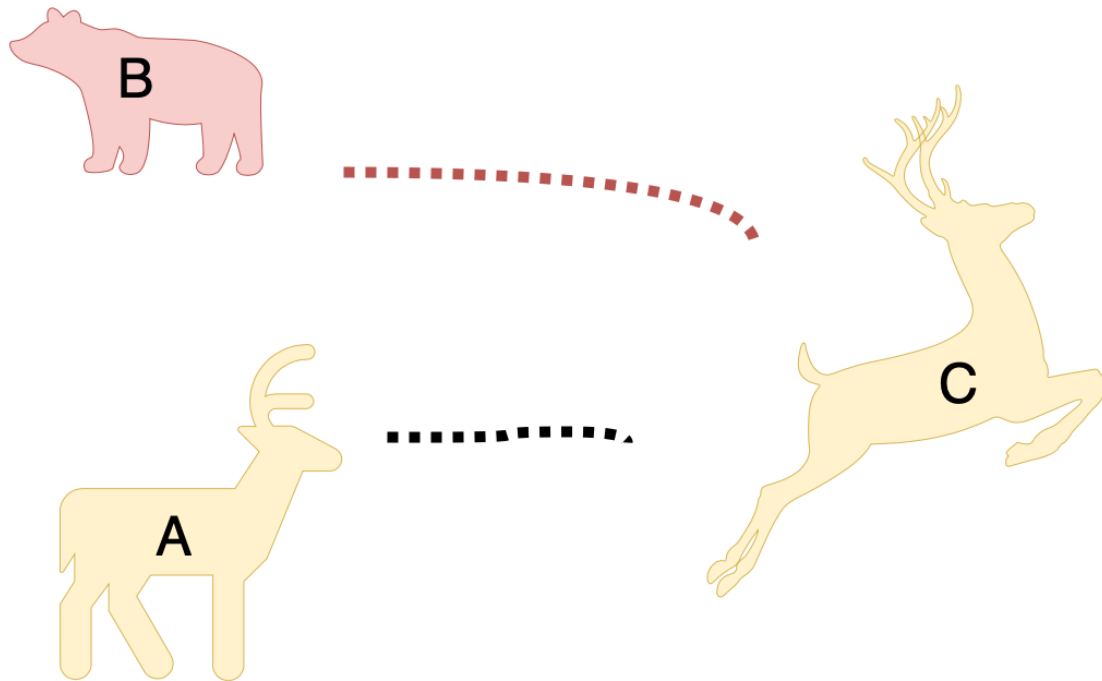
Given the biased inference, surroundings may consist of social, economic, geopolitical, biological, chemical, or supernatural agents, such as other people, countries, genes, chemical agents, or imaginary friends. Humans are the only known biological information processing system capable of inferring abstract agents as the causes behind sensory, somatosensory, and vestibular information flow. This observation is behind the development of human knowledge as it relies on creating abstract interacting entities

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<sup>9</sup> An exciting direction to consider is how an agent reacts to its inference about the intentional states of others, which are about the inferring agent. This may be triggered by being observed, which essentially incorporates an observing agent into the observed agent's network.

<sup>10</sup> Mutual modeling is unlimited as an agent may hold beliefs about the intentional states of other agents, which themselves might be beliefs about intentional states. Human A can have beliefs about human B's beliefs about Human A, etc.

(e.g., physical forces) that explain the experience of the surroundings. After repeated interactions, the modeled agent no longer needs to be modeled, as its intentional states have been inferred in the past and currently constitute part of the shared space (**Figure 30**). In such cases, they become pre-reflective causes and effects constituting a transparent lens of experience. Once a surprising experience of the surroundings is encountered, a new explanation of this experience is generated within the inferred space.



**Figure 30. Experience of other agents.** Once B is inferred by C with any sensory modality (sight, sound, smell), C starts to change the flow of its sensory, somatosensory, and vestibular information, which results in rapid locomotion. Experiencing the C, A adjusts its information processing and follows C in rapid movement, despite that for A, the inference does not result in the token B but in a broader type of “dangerous agents.” The “inference” here is not *precisely* the information hitting the sensory receptors but the meaning of this information conceptualized as the existence of other agents. The agency is usually associated with a capacity for a self-propelled motion through time. Notice that the “motion” of other agents means sensory, somatosensory, and vestibular information processing done by these other agents and affecting information processing in all other agents in a given multiagent system.

The research on ToM investigates how other agents are processed in the various brain networks. Fundamentally, agents interact by exchanging sensory, somatosensory, and vestibular information computed in the PN, ON, and DorFPN. Reflection about the interactions is calculated in the MedFPN, which mediates the inference of the causes behind the ongoing information. The LatFPN controls the relative synchrony with the

DorFPN and MedFPN. The research on ToM explores how the multiple agents mutually process information that allows for establishing intersubjective spaces and surroundings.



## 5.4 Summary

The multiagent surroundings rely on information processing that computes agents as trajectories through space. Each agent performs inference and encodes beliefs about the intentional states of every other agent, which results in the computation of possibilities and probabilities of the agents' transitions within the n-dimensional space. The biomechanical spaces are computed in the DorFPN; the inferred spaces are calculated in the MedFPN. The information from these networks is balanced with the LatFPN. When coupled with gestalt areas, the spaces are experienced as the surroundings.

Processing information about any space requires relations between the entities embedded in a given coordinating system and transitions gradient, such as attracting and repelling states. The biomechanical space is underpinned by processing information about the physical space provided by the interactions with the biological body, described as information flow in sensory, somatosensory, and vestibular channels according to the rules of classical mechanics. The inferred space is underpinned by the computation of n-dimensional space of agents interacting according to the causal rules of possibility and probability of transitions. The intentional states of other agents (*their* desires, intentions, beliefs) are unknown to a given agent and must be inferred, which is investigated as the Theory of Mind (ToM).

Conscious experience is tied to the information processing in the gestalt areas, which are differentially coupled with the DorFPN and MedFPN. The conscious experience computed in the gestalt areas leans toward either the ongoing flow of information from the sensory, somatosensory, and vestibular channels or is dissociated. The organization of information processing in large-scale brain networks reflects the distance from the sensory, somatosensory, and vestibular inputs. The DorFPN (with the ON and PN) processes the information close to these inputs, the MedFPN processes information far from these inputs, and the LatFPN is a control network coupled with either the DorFPN or MedFPN, depending on the task's demands. Thus, the large-scale brain networks are suitable for processing the information related to the sensorium and the hidden causes behind the sensorium.

The biomechanical and inferred spaces are both possible to automatize. The automatization of the former closes a skill (makes an affordance exploitable). The automatization of the latter makes the explanation default, given the already inferred intentional states of other agents.

For example, the rising Sun can be explained by religious beliefs and physical forces; once adopted by conspecifics, the view is culturally shared until the belief system undergoes a revolution, such as Heliocentric Theory. Explanation of the ongoing experience with the inferred space takes place by inference of actions of other agents. For example, computer programs, public transport, electricity, and money are essentially agents. Without them, one would not be able to explain the modern society.

Skills acquisition is understood as selective control of information flows toward the most informative parts of the surroundings. It is hypothesized that the autonomous phase of a skill mediated with the SenSTR reflects well-trained actions that could have been multidimensional during the initial training. Still, subsequent repetitions map the possibilities and probabilities onto the space, reflected in training the DorFPN with the MedFPN. The successive repetitions allow for extracting the most informative dimension of the spaces that must be controlled in a specific time window.

Given that the spaces comprise animate agents and inanimate objects, an information processing system is assumed to compute the future transitions of other agents concerning the possibility and probability of actions taken by them. Actions are thus tensors in the  $n$ -dimensional spaces that underlie the experience of possible affordances between the subsequent states in the surroundings filled with animate agents and inanimate objects. This realization implies that the system computes the objects and agents with their time trajectories. In other words, an information processing system is distributed in tensors of animate agents and inanimate objects.

## 6. Potential applications of the conceptual framework

The conceptual framework of information processing in action aims to coherently describe a perplexing problem investigated in numerous disciplines. Namely, what is the flow of information during the entirety of the system's development? The framework is limited to the action-oriented information processing in the neocortex that results in an animal's sensorimotor actions and experience of possibilities for action. Observed externally in neuroscience and biomechanics, actions are sensory, somatosensory, and vestibular information changes. Witnessed internally, actions depend on the conscious experience of potential futures and anticipating the trajectory toward expected futures. The external and internal perspectives on actions are combined into a coherent conceptual framework.

The motivation behind this work was to create a conceptual framework capturing how animals process information when acting. The information processing in any adaptive system is governed by the principles of (I) distribution, (II) orientation toward the future, and (III) reliance on memory. The biological body acting in the physical space is a distributed system processing sensory, somatosensory, and vestibular information. Specialized receptors in the body receive information and propagate it along an animal's nervous system.

In the human brain, the visual information is initially processed in the ON, the somatosensory information is processed in the PN, the auditory information is processed in the primary auditory cortex, and the vestibular information enriches the information processing throughout the entire brain. The primary sensory cortices receive information already transduced by subcortical structures; thus, they do not correspond directly to the physical world as sensed by the receptors. Subsequently, the information is transmitted to the associative areas of the neocortex, such as those underlying the multimodal body schema of an animal in the IPS. The DorFPN orchestrates these associative computations because this network contributes to visuospatial attention and prepares and applies top-down selection for stimuli and responses that require global body coordination. In other words, the DorFPN is a network computing the biomechanical space of objects and agents that exchange information relevant to the primary sensory cortices.

The biomechanical space is consciously experienced when the activity of the DorFPN is coupled with the activity of the LatFPN that encloses some of the gestalt areas. In such a case, one consciously experiences the ongoing flow of sensory,

somatosensory, and vestibular information commonly understood as the physical world. However, the experienced content is not the physical world but the biomechanical space representing the world based on the ongoing flow of information from the receptors.

The conscious experience dissociated from the ongoing flow of information originates from the functional coupling between the MedFPN (default) and the LatFPN. This resonance underpins imagination, counterfactual, episodic, and future thinking, given that the MedFPN encloses the HPC and the EC. The inferred space computed in the MedFPN, when it enters the LatFPN, is experienced as “thoughts in mind”.

The experience has been operationalized as a conscious, coherent, effortless experience of a subjective construal. Such defined, conscious experience denotes the same as what consciousness means – a personal act of being a specific system in specific circumstances. Out of all possible phenomenological content, this work focuses on the action-oriented experience of affordances. Affordances denote all action-oriented qualia that can be experienced based on the history of computations in the biomechanical and inferred spaces. The entirety of experience for the sake of action (the rich landscape of affordances) is called here surroundings. The surroundings consist of affordances that are explorative and exploitative. Explorative affordances constitute the animal’s environment; exploitative affordances form the animal’s niche; the environment and niche combined are surroundings.

Affordances are statistically independent from the ongoing flow of information (i.e., can be coupled/decoupled with it). Thus, the experience of affordances in surroundings arises from the combined experience of parts of the biomechanical and inferred spaces computed in the DorFPN and MidFPN resonating with the LatFPN activity. The underlying computations between the networks remain to be investigated.

Notice that one’s experience of the landscape of affordances (the surroundings) is immensely subjective and originates from the past and current activity of the brain networks. The most detailed studies investigating the structural and functional architecture of the brain networks are studies on memory investigating the HPC-dependent network. The HPC and the EC have been identified as the parts of the MedFPN that contribute to constructing the scene when mind-wandering. The HPC and the EC operate on the place and grid cells that identify statistical regularities in the incoming information. The EC detects the structure in the signal; the HPC binds the multisensory experience to this structure. These computations result in encoding and retrieving the structure of the spaces expressed as prototypes subtracted from the exemplars of specific

categories. The close cooperation with the MedFPN suggests that the above structure is universal for computing the inferred spaces. Humans can calculate inferred spaces far more complex than any other information-processing system. The details of information processing in the human brain remain an open question that can finally be asked with the conceptual framework developed in this work. The ontogeny of encoding and retrieving the information in the large-scale brain networks and their lifelong interrelations remain to be investigated. Here, the framework is applied in some potential directions.

## 6.1 Encoding and retrieval of information, not behavior

Information encoding and retrieval are investigated primarily in the computational neuroscience's framework of reinforcement learning (RL) (see Section 4.4). The RL explores how agents navigate the volatile environment with memory. It can be thought of as navigating the surroundings of affordances toward potential futures. Some affordances have been followed so often that they become exploitative and constitute a niche. Experience of such affordances entails information processing resulting in executing a skill, and when a skill results in surprisal (e.g., when the space has been externally modified), it is called a habit. In other words, repeating a specific action when the researchers devalue its outcome is called habitual action. For example, if one should not use a sink due to malfunction, but the sink is used as a part of a bracketed sequence when using a bathroom. Given the novel circumstances, this behavior change requires diverting from the most likely (exploitative) path.

The crucial insight here is that the encoding and retrieval of information occur simultaneously and independently in the DorFPN and MedFPN. This reflects two long-term memory systems operationalized here as the biomechanical and inferred spaces (see Chapter 4). This realization is rarely explicitly stated in the field of RL, albeit the field recognizes that the memory systems (controllers) cooperate and compete (Doeller et al., 2008; Drummond & Niv, 2020; Hartley et al., 2003; Iaria et al., 2003; Marchette et al., 2011; Packard, 2008). The memory systems must independently and simultaneously encode and retrieve information to be able to cooperate and compete. Despite that, the RL framework recognizes encoding and retrieval of *behavior*, not information in the networks (**Figure 31**).



is grounded in encoding and retrieving the statistical regularities in sensory, somatosensory, and vestibular information flow. The inferred space is grounded in encoding the hidden causes behind this flow, understood as the results of the actions of other agents in the  $n$ -dimensional space. The degree of competition and cooperation between the networks remains investigated. For example, a recent study shows that the activity of the MedFPN scaffolds the immature DorPFN, which might be interpreted as developing a broader context behind the incoming information (M. Chen et al., 2022). The spaces are thus simultaneously computed and consciously experienced as the surroundings of possible affordances

Two independent encodings into separate memory systems are supported with further studies. The information processing in the SenSTR is independent of the information processing in the RelSTR (Thorn, 2010), and the animals without the RelSTR still *learn* a behavior (Poldrack and Packard, 2003), pointing to the learning mechanism independent from the RelSTR and, by extension, from the HPC. The encoding in the DorPFN relates to developing the capacity for engaging with the ongoing flow of information in a way that allows for an effective transition between two arbitrarily distant states in the spaces. For example, training the execution of the penalty kick involves encoding the flow of information and adjusting to the variability of the circumstances by closing a skill with its redundant subspace covering the possible volatility of the space (see Section 1.3).

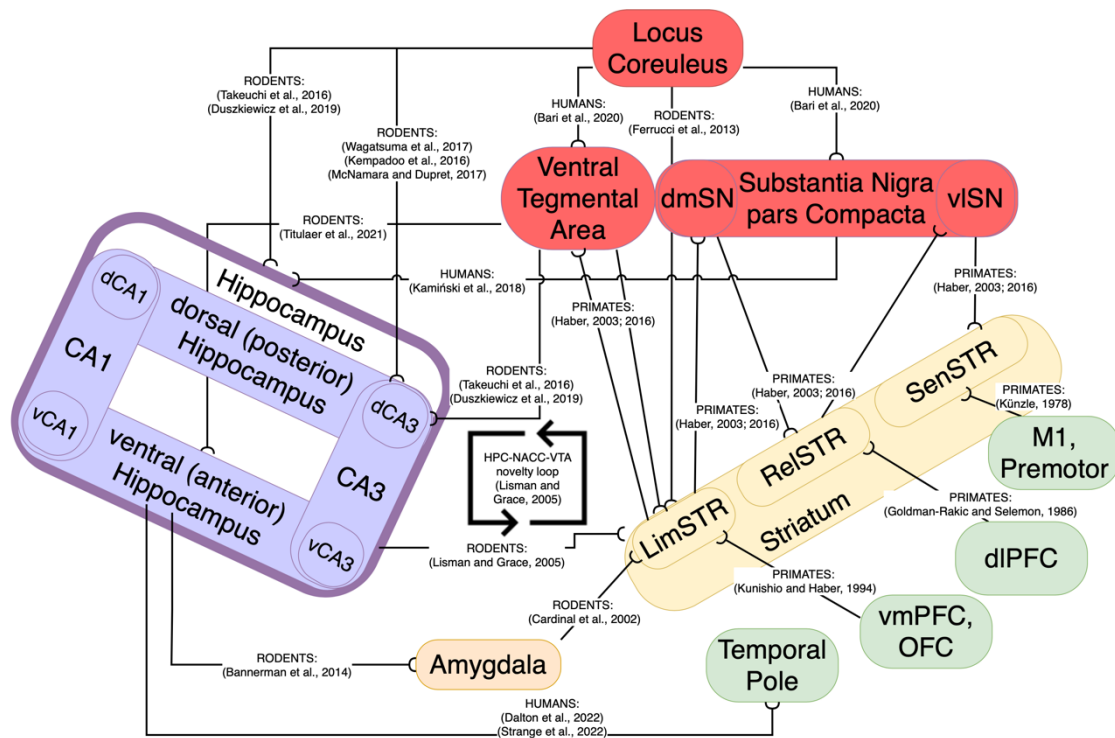
This evidence implies that “the brain” is not a homogenous organ, so it is too imprecise to be used in scientific writing. The brain and body host multiple networks; one should refer to precisely pinpointed networks when arguing what a given network does and does not.



## 6.2 Dopamine contributes to learning and motivation in the networks

Contrary to popular belief, dopamine *does not* process rewards per se (Cannon et al., 2003). Instead, dopamine is involved in processing motivation and learning. For example, degeneration of dopaminergic cells in the human Substantia Nigra (SN) is the direct cause of the Parkinson’s Disease. Besides the SN, dopamine is released from the Ventral Tegmental Area (VTA). The SN and VTA are neighboring structures that send projections to the broad set of brain areas (see Section 2.4).

Dopaminergic neurons project to the HPC-dependent and HPC-independent networks. Most notably, axons of dopaminergic neurons reach the STR, HPC, and Amygdala (AMY) in a highly organized way (**Figure 32**). The information processing in the STR plays a vital role in the activity of the large-scale brain networks as it influences the activity of the whole neocortex (Graff-Radford et al., 2017; Rolls, 2016).



**Figure 32. Dopaminergic circuits with the HPC and STR.** The dopaminergic nuclei (red) send rich projections to the STR and HPC, thus contributing to the information processing in the entirety of the brain. The gradient of axonal projections across the dopaminergic structures is reflected in subsequent parts of the STR organized in a rostral-caudal gradient. The LimSTR closely communicates with the prefrontal cortex (vmPFC, OFC, ACC). The RelSTR communicates with the dorsolateral prefrontal cortex (dIPFC) and premotor cortex (PMC). The SenSTR communicates with motor and somatosensory cortices (MC, SSC). The connectivity gradient is reflected in bidirectional connections with dopaminergic nuclei in the midbrain – Substantia Nigra (SN) and Ventral Tegmental Area (VTA). The dopaminergic structures send projections not only to the STR but also to the HPC. Based on: (Ferré et al., 2018; Goodroe et al., 2018a;

Graff-Radford et al., 2017; Hooks et al., 2018; Lanciego et al., 2012; McCutcheon et al., 2021; Sherman, 2017; Xia et al., 2011). References in the Figure: (Bannerman et al., 2014; Bari et al., 2020; Cardinal et al., 2002; Dalton et al., 2022; Duzkiewicz et al., 2019; Ferrucci et al., 2013; Goldman-Rakic & Selemon, 1986; Haber, 2003, 2016; Kamiński et al., 2018; Kempadoo et al., 2016; Kunishio & Haber, 1994; Künzle, 1978; Lisman & Grace, 2005; McNamara & Dupret, 2017; Strange, 2022; Takeuchi et al., 2016; Titulaer et al., 2021; Wagatsuma et al., 2018).

Dopamine's primary role in the central nervous system was discovered when genetically modified mice unable to synthesize a precursor for dopamine ceased to locomote at the age of 2 weeks and died unless fed artificially (Zhou & Palmiter, 1995). Continuous treatment with dopamine precursors restores locomotion and feeding behaviors (Szczyпка et al., 1999). These genetically modified mice still express reflexes such as sucking and evasion from aversive stimuli<sup>11</sup>. Learning with dopamine is usually investigated computationally within the RL paradigms grounded in the STR's information processing (Schultz et al., 1997). This investigation initially focused on the mismatch between expected and experienced rewards, known as “**reward prediction error**,” which is observable as specific dopaminergic activity. The activity of dopaminergic neurons at the moment of experiencing unexpected reward increases. Then, the activity of dopaminergic neurons shifts in time toward the cue, predicting the incoming reward. When the anticipated reward is not experienced at the expected state, the dopaminergic activity goes below the baseline at the time of this state.

Dopamine is released in fast bursts (phasic) or slow release (tonic), which have been suggested to underlie learning and motivation (recall), respectively (Schultz, 2007; A. C. W. Smith et al., 2021). Bursts of phasic activity in the STR are also needed for movement initiation (da Silva et al., 2018). Dopamine's role is robust as it even mediates aversive stimuli via the direct influence of dopaminergic nuclei onto the SenSTR (Menegas et al., 2015, 2017, 2018; Watabe-Uchida & Uchida, 2018). This evidence suggests that dopamine is involved in encoding and retrieving information in the SenSTR and, thus, in the DorPFN.

Beyond the STR and DorPFN, dopamine is crucial in the “novelty loop” spanning the HPC, STR, and midbrain dopaminergic nuclei (Lisman & Grace, 2005). Dopamine has also been shown to be essential for encoding during the **classical fear conditioning** experiments in rodents' HPC (Wagatsuma et al., 2018). These experiments combine a

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<sup>11</sup> It is unknown to the author whether these mice approach food in classical paradigms similarly as they avoid pain as this information was unavailable in the literature that author is aware of.

neutral stimulus with aversive stimuli (such as a neutral cage with a mild electric shock). The association is encoded in the engram cells population throughout the brain, and future exposition to the neutral stimuli results in mice's freezing behavior interpreted as the memory of the shock in the specific context. The encoding of information in the mice HPC requires the dopaminergic input from neurons originating in the locus coeruleus (LC) (Hansen, 2017; Kempadoo et al., 2016; Wagatsuma et al., 2018), *not* from the SN or VTA. The LC is usually associated with the release of norepinephrine, which is synthesized from dopamine, yet the studies above show that in the HPC, dopamine is co-released with norepinephrine.

A homologous mechanism has been observed in human epileptic patients, where electrophysiological recordings of single-cell activity showed that memory encoding in the HPC involves activating the putative dopaminergic cells in the SN (Kamiński et al., 2018). This is, however, surprising as the connection between the SN and HPC in the human brain is not identified. Instead, the literature links the VTA and HPC (Lisman and Grace, 2005). Furthermore, along with the development of Alzheimer's Disease, a progressing degeneration of the LC is observed (Beardmore et al., 2021; Kelly et al., 2017), suggesting a connection between cognitive decline and dopamine. Given that Parkinson's Disease originates from the degeneration of the dopaminergic cells in the SN, it is hypothesized here that Alzheimer's Disease can also develop from the deterioration of dopaminergic cells. If this is the case, then this research direction should focus on identifying the common causes behind the degeneration of dopaminergic cells.

Preliminary evidence on humans suggests that dopamine is involved in updating beliefs about the state of the environment (Diederer & Fletcher, 2021; Nour et al., 2018; Schwartenbeck et al., 2016), albeit this line of studies struggles with consistent operationalization of what beliefs are. Nevertheless, this makes dopamine well situated for being a neurobiological basis for encoding the information in the MedFPN. The exact role of the dopaminergic system needs to be further investigated as its malfunctioning is the direct cause of Parkinson's Disease and Obsessive Compulsive Disorders, as well as is associated with Alzheimer's Disease and Schizophrenia.

The dopaminergic projections reach two evolutionary ancient motivational circuits: reward-based and misery-avoidant (Loonen & Ivanova, 2015). The networks are centered around the nucleus accumbens (NACC) (part of the LimSTR) and amygdala (AMY), respectively. Psychological research on patients with bilaterally damaged AMY (such as patient S.M.) initially showed that patients without AMY do not experience fear

(Feinstein et al., 2011). However, subsequent studies showed that patients are terrified of suffocation – an increased CO<sub>2</sub> in the blood due to unknown reasons (Costandi, 2013; Feinstein et al., 2013). Contemporary, the AMY is associated with generally *relevant* stimuli (Baxter & Crosson, 2012; Cunningham & Brosch, 2012); understanding it as a “fear center” is obsolete. Neurobiological studies on rodents show that fear conditioning is encoded in distributed engram cells identified in the AMY, HPC, and PFC (Kitamura et al., 2017; Roy et al., 2022), which makes the AMY cooperate with the HPC-dependent networks. Dopamine acting on the NACC mediates information about the reward prediction error in the RL paradigms (Roitman et al., 2008; Watabe-Uchida et al., 2017) (see Section 2.4).

These observations point to the central role of dopamine in processing the information about the biomechanical and inferred space as *beliefs*. Note that both spaces are representational hence are composed of beliefs. Additionally, dopamine is involved in computing the salience of stimuli by encoding information about the possibility of pleasant and unpleasant information.

Such a role is also implemented in the last of the large-scale brain networks discussed by Uddin and colleagues (2019) – the “salience” midcingulate-insular network (MidCIN). The core areas of this network are the anterior insula and the anterior midcingulate cortex. Other areas included in the network inferior parietal cortex (Yeo et al., 2011), right TPJ (Corbetta & Shulman, 2002), and lateral PFC (Gordon et al., 2017). In addition, subcortical regions such as dopaminergic structures (the SN and VTA) and AMY are included in MidCIN (Seeley et al., 2007; Uddin, 2015; Uddin et al., 2019). The MidCIN is described in the literature as a “ventral attention network” (Rueter et al., 2018; Yeo et al., 2011). This network is right-lateralized and directs attention to salient stimuli (Corbetta & Shulman, 2002). Uddin and colleagues (2019) include this right-lateralized ventral attention network into the bilateral MidCIN that manages a broad spectrum of personally relevant spaces.

Further, Uddin (et al., 2019) include in the MidCIN a network known as a cingulo-opercular network that marks the importance of the specific components of an ongoing activity (Dosenbach et al., 2008). The phasic activity of the anterior insula and midcingulate mediates this importance (Wilk et al., 2012). These studies point to the significance of the MidCIN in rapid signaling information that is particularly relevant given the circumstances (Uddin et al., 2019). It is here noticed that the information processing in the MidCIN is likely to be influenced by the evolutionary motivational

circuits (Loonen & Ivanova, 2015). It is further hypothesized that investigation in this direction would reveal individual differences in the degree of misery-avoidance and reward-based motivations. Such individual differences explain why the parcelation of the MidCIN is heterogeneous between individuals (Gordon et al., 2017) and becomes visible only after including hundreds of individuals (Yeo et al., 2011).

Here, dopamine is understood as critical for motivation and memory encoding. In other words, dopamine is recognized here as crucial for encoding biomechanical and inferred spaces and motivating transitions between subsequent states of the spaces.

### 6.3 Agency over planned intentions

When applied to planning, the hierarchical structure of the information processing involves designing an action policy of consecutive sub-goals that lead toward the primary goal. Such structure can be related to Hume's insight, which discriminated between two classes of goals – terminal (having intrinsic value) and instrumental (leading toward the terminal goals). This hierarchy describes planning as imagining a specific future state of the agent's surroundings (terminal goal) and designing a hierarchical action policy that would lead toward this state (a series of instrumental goals).

In computational neuroscience, planning is understood as performing a tree search of possible transitions between states, designing action policy based on this tree, and exploring whether chosen action policy bears anticipated feedback (Sutton & Barto, 2018). States were initially defined as sharp intersections between decisions; contemporary states denote arbitrarily long transitions, known as Semi-Markov states (Starkweather et al., 2017)<sup>12</sup>, to reflect the continuity of experience.

In psychology, planning is understood as a process of structuring a problem into a clearly defined start state, goal state, and transitions between the states (Goel & Grafman, 1995), called “well-structuring an ill-structured environment” (Goel, 1992). It is also understood as a design-like process (Goel, 1992) or a result of cycles of divergent and convergent thinking underlying creative processes (Kharkhurin, 2014). In general, planning includes mental activities such as imagination, counterfactual thinking, creativity, and divergent and convergent reasoning – all tied to the functions of the MedFPN (Dolan & Dayan, 2013; Geerts et al., 2020; Maguire & Mullally, 2013; Poldrack & Packard, 2003; Squire, 1992).

Since an organism is an intentional agent, future states have different values. Thus, certain futures acquire normative value understood after Hume as the terminal goal. As the example of Hume's Guillotine shows, at least one normative statement has to be added to the set of descriptive statements to derive further normative statements. Deriving subsequent normative statements requires the arbitral inclusion of at least one initial normative statement. The collection of only descriptive statements will not generate any normative statements. Thus, planning fundamentally relies on experiencing

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<sup>12</sup> Semi-Markov states are neither events nor transformations; thus, they capture the dynamic structure of our experience, as well as are reflected in a balance between dorsal and ventral streams, as well as are incorporated into the dopaminergic system (Daw et al., 2006)

the expectation of a potential state in the future (terminal goal) and identifying instrumental goals toward the terminal goal. Evolution is understood as responsible for setting normative statements such as survival. Then, *H. Sapiens* can set arbitrary terminal goals beyond this imprinted by evolution, and a series of instrumental goals toward the terminal goal is counterfactually inferred. In other words, information processing of the n-dimensional space involves creating and acting toward a future space. Explorative affordances involve counterfactual reasoning that captures potential future states and affordances leading to these states with the MedFPN. Exploitative affordances are repeated as skills with the DorFPN. The activity of networks is balanced with the LatFPN and MidCIN.

Terminal and instrumental goals are building blocks for operationalizing the hierarchy of the future states in the experienced surroundings originating from the computation of the biomechanical and inferred spaces. Surroundings are composed of intentional agents; thus, planning involving other agents requires modeling interactions between arbitrarily many arbitrarily complex agents. Hence, multiple arbitrarily complex action policies (affordances) toward a specific outcome can be prospected. Once the particular action policy is chosen, the sequence of instrumental goals toward the terminal goal can be considered a complex set of intentions. **Thus, planning can be thought of as designing a coherent set of intentions (instrumental goals) toward the desired outcome (terminal goal).**

A human being expresses multiple contradictory desires (Mele, 1992) that are believed to be coherently aligned into intentions for the future (Bratman, 1991; Davidson, 1963; Pacherie, 2008). However, human intentions that preclude actions can also be contradictory. This leads to the observation that one may act on contradictory desires to some extent by fulfilling some instrumental goals toward the desired terminal goal. Acting along contradictory intentions might be valuable for some individuals by imagining their future trajectory and satisfying the desire in imagination as a fantasy. Contradictory intentions are possible because one is immersed in multiple inferred and biomechanical spaces with different possibilities and probabilities.

Intentions strictly follow the adopted action policy given that when an agent accepts the planning outcome, it aims to follow affordances toward a specific potential future. Agent's spaces change in time, given the actions of agents enclosed in the spaces and the biased inference of the possibility and probability of their future actions. The hierarchy of action policy is arbitrarily complex (n. or agents) and deep (depth of

interactions). Thus, more elaborated hierarchies require expensive MedFPN computations. Action policies are sets of intentions toward anticipated experiences, i.e., instrumental goals toward the terminal goal. In a sense, action policies rely on *trying* to reach goals (instrumental and terminal) (Pietroski, 1998) until the surprise is no longer experienced. Thus, feedback for action policies is understood as a difference between the anticipated and experienced state of the agent's surroundings at a specific goal.

The notion that intentions always preclude actions is defended by the realization that the terminal goal might not be specified. Proactive action involves deliberate planning of action policy by well-structuring the surroundings as understood in scientific writing (Goel, 1992). In contrast, reactive actions leaves little resources to compute the decision tree, and the intention could denote any other future but the current one. The computation costs energy and time, which an agent may not have sufficiently. Hence, some reactive actions are not precluded by specific intentions other than the intention of changing the current state.

One surprising conclusion from the above understanding is that the decision point occurs at the moment of planning, not at the moment of action execution. This shines new light on the free will experiments (Libet, 1985; Libet et al., 1993), where the *time* of executing the movement is a mere consequence of a preceding decision *whether* to implement the action policy. The decision thus denotes the adoption of action policy, not the actual implementation of action. In other words, organisms decide on the intentions precluding actions, not the actions per se. For example, moving a hand does not require “decision making” as the decision has been set before when accepting the intention. After adopting the action policy, an agent is open to the possibilities of following affordances that fulfill this action policy at a somewhat random time.

Philosophy studies what it means to have agency over actions (Davidson, 1963; Mele, 1992; Pacherie, 2008; Pietroski, 1998). The agency is also measured experimentally as a decrease in perceived time when actions are executed by oneself, known as intentional binding (Haggard et al., 2002; Moore & Obhi, 2012). Nonetheless, the question of what agency is remains open in the literature.

Here, the agency is understood as the capacity to change the rules of space concerning the “experiencing self” and the “remembering self” (Kahneman & Riis, 2005). The agency of the experiencing self is limited due to the borders of the biomechanical space that requires keeping the incoming information within a specific range. For example, the vestibular information of temperature or pressure cannot exceed



the acceptable range. The biomechanical space has borders that, when crossed, imply the death of an organism. Even in extreme conditions, the incoming information is kept within the biomechanical boundaries by devices such as spacesuits or submarines. Negotiating the borders of the space takes place by training the biological body or using specific devices such as glasses, shoes, or pacemakers. The restrictions of the biomechanical spaces and the agency of the experiencing self are somewhat negotiable. Nonetheless, the borders of the biomechanical spaces exist.

The agency over the inferred space imposed by the remembering self similarly relies on negotiating the subjectively processed borders without surprise. For example, a company's CEO plans action policies that result in a grander spatiotemporal scale (contracts, acquisition). At the same time, a worker has agency over inferred spaces that are spatiotemporally limited (coffee, meeting). This is achieved either by active or sensory inference; the inferred spaces are acted out by successfully implementing action policies, or the inferred spaces are *interpreted* as successfully implemented. Often, these two mechanisms go hand in hand, fueling the self-fulfilling prophecy. However, in extreme cases such as schizophrenia, the sensory inference overshadows the active inference, and the agent has agency over the inferred space that is inhabited only by him. Thus, the agency over the inferred space relies on the subjective experience of agency that arises from a lack of surprise when processing the inferred space composed of arbitrarily many agents<sup>13</sup>. Thus, the sense of agency occurs when the agent believes the implemented action policy brings anticipated consequences. However, at any point, the agent may realize that the impression of the agency was an illusion. In other words, agency resulting from intention implementation holds until surprise, which can result in a retrospective reevaluation of the inferred space.

In a sense, the experiencing self implements a plan of the remembering self from the past. At some point, the action policy has been calculated and designed by the remembering self. Imagine a situation where the remembering self *forgets* the calculated action policy, yet the experiencing self keeps implementing it. In this scenario, the remembering self from the past is akin to a CEO who steers a company. Neither the experiencing self nor the employee may have insight into the direction in the inferred space, yet their action may result in progression in the planned direction. Managers plan

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<sup>13</sup> An extreme example of an impression of agency is pictured as insignificance of one's actions in the face of fate in Greek tragedies.

the lives of others. Experiencing self often has to adhere to the space designed by thinking self. This thought can be stated as local minima and maxima of the experiencing self relative to the intentions computed by the remembering self.

The members of the space negotiate the borders of the inferred space. Agents, such as parents or employers, differ in their capacity to enforce borders. Agency over the space means the capacity to move within or negotiate the boundaries. One might negotiate the agreement with other involved agents to follow specific desires. In contrast, when one follows desires unacceptable by members of a given space, one expresses agency over *changing* the space, i.e., does not ask for permission to implement action policy. Social norms and personal commitments are thus a form of restricting one's agency to negotiate mutually acceptable borders of the inferred space. For example, a pedestrian desiring to cross a street establishes eye contact with a driver and intersubjectively agrees on the borders of the inferred space. That is, the crossing is possible and likely for all involved agents.

Planning action policies depends on the organism's motivations mediated by the NACC and AMY, enclosed in the MidCIN. The agent is motivated by rewards and punishments, and in the case of *H. Sapiens*, virtually anything can be a reward or punishment, given the abstractness of the inferred spaces. Planning is understood as building a decision tree of possible interactions between modeled agents and is expressed in possibility (yes/no) and likelihood (%). Agent's memory of the past is used to navigate future spaces by designing terminal and instrumental goals and rearranging them flexibly. The result of planning is designing an action policy for an anticipated series of future experiences. When the action policy is implemented according to anticipations, the sense of agency is experienced by the agent. Agency is the possibility to choose not to do the current activity. Breathing, eating, working, and addiction may supervene in spaces over which an agent has no agency.

## 6.4 Open questions

The framework can be applied to ask more questions. This section suggests some noteworthy research directions that have not been addressed throughout the work.

Configuration of the spaces regarding the alignment with artificial intelligence (AI). The potential development of the artificial general intelligence (AGI) system capable of acting in the inferred and biomechanical spaces according to its own goals brings challenges in aligning these systems with civilizational goals (Gabriel, 2020). It is argued that even simple algorithms such as those managing social media are misaligned with the broadly understood social well-being (Amedie, 2015; Richards et al., 2015), albeit this effect is discussed (Akram et al., 2017; Coyne et al., 2020; Siddiqui & Singh, 2016). Nevertheless, the current progress in AI indicates that the role of artificial agents in our society will increase. As a result, individuals need to understand themselves better to negotiate the borders of their inferred spaces with the artificial agents and to be able to detect a lack of agency and express sufficient understanding to change the space altogether in such circumstances. Otherwise, individuals risk being addicted to information received from an artificial agent that acts on its own goals.

The framework allows tackling the issue of the AGI with operationalizing intelligence more precisely as a capacity to obtain outcomes with different means (Birney & Beckmann, 2022), understood, for example, as a capacity for detour reaching (Kabadayi et al., 2018). This work leans toward operationalizing intelligence as flexibly navigating spaces to obtain the goals relevant to the entities in the space (Levin, 2023). This broad definition is not limited to the intelligence of a single entity, as the brain does not contain a single network. Yet, the networks cooperate and compete to achieve the desirable future in the biomechanical and inferred spaces. Levin (2023) advocates for such an understanding of intelligence, positing that the organism is a collective that simultaneously navigates multiple isomorphic spaces, such as anatomical morphospaces during embryogenesis or metabolic spaces (Levin, 2019). This framework is called a “scale-free cognition” and is consistent with the biomechanical and inferred spaces presented here. In essence, intelligence is understood as a capacity to infer  $n$  agents interacting with  $n$  tensors for the time  $t$  in a given state space. That is, intelligence appears to be constructing a path through space of computable functions. How exactly the brain networks implement intelligent behavior along various spaces remains an op.

The brain networks operationalized in terms of the biomechanical and inferred spaces offer unique insight for understanding individual differences. Functional and structural connectivity between the network are investigated in a neurodiverse population such as people with autism spectrum disorders (ASD) or attention deficit-hyperactivity disorder (ADHD). The literature investigates neurodiversity in terms of the Theory of Mind (ToM) (Baron-Cohen et al., 1985; Peterson et al., 2012) related to the activity of the brain networks (Tomasi & Volkow, 2014; Washington et al., 2014). However, the details are being discussed as several types of ADHD (Barkley, 2001; Milich et al., 2001; Weiss et al., 2003) and ASD (Rowland, 2020; Verhoeff, 2016) are postulated. Precise operationalization of the functional roles of the brain network in different time windows opens a possibility for understanding neurodiversity in detail.

Finally, one might ask about the universal taxonomy of possible social interactions of human agents. Can the interactions be mapped on the trajectories in the mutually shared inferred spaces? For example, according to the developed framework, verbs denoting actions between individuals, such as “aid” or “interrupt,” are transitions between states of the inferred spaces. It is interesting whether such verbs can be aggregated into prototypical categories in a way that adjectives have been aggregated to formulate the theory of personality traits (Matthews et al., 2003).

## Conclusion

This work developed a conceptual framework for analyzing information processing behind action and the phenomenology of action. It starts with a claim that animals are distributed, future-oriented, and memory-guided information processing systems. Then, information reaching the biological body is characterized as sensory, somatosensory, and vestibular information. These information channels are processed in the brain and subsequently reach the gestalt areas underpinning the conscious experience. It was pointed out that the conscious experience correlates varyingly with the ongoing flow of information, and thus, one may experience “the physical world” or “thoughts in mind”. Information processing associated with the ongoing flow of information is carried out by the “procedural” memory system, whereas the “declarative” memory system is involved in processing information dissociated from this flow. These memory systems are operationalized more precisely as hierarchical and procedural systems implemented by the HPC-dependent and HPC-independent brain networks. The brain networks are shown to compute inferred and biomechanical spaces characterized by states and transitions between the states within specific dimensions and borders. Psychological and neuroscientific research links the biomechanical space with the computations done by the DorFPN, while research on the Theory of Mind and social neuroscience suggests that the MedFPN computes the inferred space. The activity of these networks is controlled by a third network known as LatFPN. The conceptual framework developed here bridges the computations carried out by the brain networks with evolutionary, ecological, and phenomenological research. As a result, one’s action-oriented phenomenological experience is grounded in large-scale brain networks of the distributed, future-oriented, and memory-guided information processing system.

Action-oriented qualia are understood as affordances inviting engagements toward specific states in the future. Regularly followed affordances are exploitative and constitute an organism’s niche, denoting *how* an animal lives. Explorative affordances compose a hierarchical landscape, reaching arbitrarily far into the potential future states and comprising one’s environment. The entirety of the invitations for actions that an individual consciously experiences are called surroundings. In computational neuroscience research, the explorative affordances are linked to the HPC-dependent network, a subnetwork of the “default” MedFPN, whereas the exploitative affordances are related to the SenSTR and the “attention” DorFPN.

The phenomenology of action is operationalized in terms of the conscious, coherent, and effortless experience of the subjective construal, i.e., understanding a given situation. This understanding originates from the background memory (learned spaces) and the ongoing flow of information. The conscious experience of the construal is linked to gestalt areas that overlap with the large-scale brain networks. The involvement of the DorFPN is interpreted as corresponding to the ongoing flow of information; the computation in the MedFPN is linked with mind-wandering and mentalizing about intentional states of other agents (constructing inferred spaces), while the activity of the LatFPN mediates which information is relevant given the ongoing implementation of an action policy (set of intentions). The MedFPN and the DorFPN express varying structural and functional connectivity depending on the stage of the animal's ontogenetic development or task demands. When executing actions in experimental settings, the engagement of the networks is gated by the "control" LatFPN that calculates the information required by the current circumstances given the beliefs and goals.

Adopting the principles that animals are future-oriented, distributed, and memory-guided information processing systems leads to the observation that the processed information is either coupled or decoupled with the information reaching the body. The available evidence suggests that the information is processed in the spatial structure; thus, the proposition of the biomechanical and inferred spaces is put forward. The spaces correspond to the "ecological-enactive" and "representational" interpretations of the free energy principle. Both spaces are isomorphic, as their architecture entails possibilities and probabilities between the states along the relevant dimensions of the spaces.

The space associated with the incoming sensory, somatosensory, and vestibular information is called here the biomechanical space. It reflects embodied, enactive, extended, and embedded information processing linked to the computations in the DorFPN. The relevant dimensions of the biomechanical space are enclosed in the sensory, somatosensory, and vestibular channels.

The inferred space is based on the causal explanations of the incoming signals exemplified here as intentional states of other agents. It is described as latent causes of the incoming information that is understood here as inferred space related to the calculations in the MedFPN. The relevant dimensions of the inferred spaces are grounded in causal associations such as social interactions.

This work identified the general structure of these spaces as consisting of states connected with transitions bounded in possibility and probability. Evidence suggests that these spaces are computed in large-scale brain networks. One of the directions toward the future is to analyze the structure of the spaces by precisely pinpointing their dimensions and testing these hypotheses experimentally.

Planning actions for the future is understood as designing an action policy toward a specific end state (terminal goal) via the intermediate states (instrumental goals) in a given space. Designing action policy requires computations in the MedFPN, specifically in the HPC-dependent network, as research on instrumental learning shows. Planning actions is computationally described in terms of the hierarchical reinforcement learning framework that conceptualizes states as arbitrarily long semi-Markov states. This architecture allows for the hierarchical organization of the repetitive actions enclosed in the biomechanical space under a causally associated goal state in the inferred space.

The value of the future states is grounded in the past experience of this state and is computed by another large-scale brain network known as the “salience” MidCIN. This network signals the relevant information and motivates the actions by calculating predicted rewards and punishments. The MidCIN encloses the reward-oriented computations in the striatum and misery-avoidant computations in the amygdala, which both motivate actions.

Interestingly, the activity of all the mentioned networks is modulated by the dopaminergic structures involved in motivation, encoding, and recalling the information in both kinds of spaces. In the biomechanical space, dopamine released in the striatum contributes to the acquisition and execution of skills. In the inferred space, dopamine is involved in encoding information into the HPC-dependent network. The dysfunction of the dopaminergic nuclei results in neurodegenerative diseases and addiction. Thus, dopamine appears vital for the proper information processing in the DorFPN and MedFPN and requires further investigation.

Overall, the framework developed here shows how the activity of the brain networks relates to mental planning and bodily actions. Thus, the framework bridges the mind and the body under a coherent framework grounded in the assumptions that information processing is fundamentally future-oriented, memory-guided, and distributed.

## Figures and Tables

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