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COGNICIÓN Y REPRESENTACIÓN INTERNA DE ENTORNOS DINÁMICOS EN EL CEREBRO DE LOS MAMÍFEROS

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PRESENTADA POR

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COGNITION AND INTERNAL REPRESENTATION OF DYNAMIC SITUATIONS IN MAMMALS’ BRAIN

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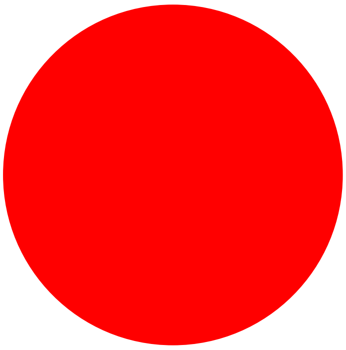

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PROGRAMA DE DOCTORADO EN BIOLOGÍA

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Table of contents

Figure list

Resumen

COGNICIÓN Y REPRESENTACIÓN INTERNA DE ENTORNOS DINÁMICOS EN EL CEREBRO DE LOS MAMÍFEROS

El tiempo es una de las dimensiones fundamentales de la realidad. Paradójicamente, los fenómenos temporales del mundo natural contienen ingentes cantidades de información redundante, y a pesar de ello, codificar internamente el tiempo en el cerebro es imprescindible para anticiparse a peligros en ambientes dinámicos. No obstante, dedicar grandes cantidades de recursos cognitivos a procesar las características espacio-temporales de entornos complejos debería ser incompatible con la supervivencia, que requiere respuestas rápidas. Aun así, los animales son capaces de tomar decisiones en intervalos de tiempo muy estrechos. ¿Cómo consigue hacer esto el cerebro? Como respuesta al balance entre complejidad y velocidad, la hipótesis de la *compactación del tiempo* propone que el cerebro no codifica el tiempo explícitamente, sino que lo integra en el espacio. En teoría, la compactación del tiempo simplifica las representaciones internas del entorno, reduciendo significativamente la carga de trabajo dedicada a la planificación y la toma de decisiones. La compactación del tiempo proporciona un marco operativo que pretende explicar cómo las situaciones dinámicas, percibidas o producidas, se representan cognitivamente en forma de predicciones espaciales o *representaciones internas compactas* (CIR), que pueden almacenarse en la memoria y recuperarse más adelante para generar respuestas. Aunque la compactación del tiempo ya ha sido implementada en robots, hasta ahora no se había comprobado su existencia como mecanismo biológico y cognitivo en el cerebro.

El primer objetivo de este estudio fue demostrar experimentalmente que la compactación del tiempo es una estrategia cognitiva presente en el cerebro humano. Para ello se recogió una muestra de 410 participantes que realizaron una tarea de clasificación por ensayo y error, diseñada para modular el ritmo de aprendizaje bajo las asunciones de la compactación del tiempo. Los participantes debían encontrar una regla oculta que asociase estímulos estáticos y dinámicos mostrados en una pantalla de ordenador, con las teclas de flecha arriba y abajo del teclado. Según la teoría, debería ser posible interferir con el proceso de aprendizaje mediante la exposición previa a escenarios estáticos que coincidiesen o no con las CIRes de situaciones dinámicas. Las asociaciones formadas en esa primera fase de estímulos estáticos se almacenarían en memoria, y podrían favorecer o dificultar el rendimiento durante una segunda fase compuesta por estímulos dinámicos. Los resultados revelaron que la compactación del tiempo es una estrategia cognitiva en los hombres, cuyo aprendizaje se moduló según lo

previsto. Sin embargo, las mujeres no mostraron dicha modulación, a pesar de que su rendimiento fue comparable al de los hombres del grupo control. Además, las mujeres verbalizaron la regla de asociación en términos de colisiones o futuras interacciones, indistintamente de su rendimiento, mientras que sólo los hombres que resolvieron la tarea rápidamente usaron esos términos. Esto implica que la compactación del tiempo es un mecanismo cognitivo predominante en hombres, y que las mujeres recurren a ella a la vez que a otras estrategias dentro de un repertorio más amplio.

En este trabajo también se ha estudiado la edad de aparición de la compactación del tiempo. Para ello se recogió una muestra de 386 niños y niñas, entre 8 y 11 años de edad. La tarea que realizaron fue una versión simplificada y equiparable a la descrita en adultos. Los resultados revelaron que la compactación del tiempo no es aún un mecanismo cognitivo saliente antes de los 11 años, aunque el rendimiento similar mostrado durante las fases estáticas y dinámicas, indistintamente del género y la edad, sugiere que podría estar funcionando como estrategia basal de fondo.

El segundo objetivo de este estudio fue describir matemáticamente el comportamiento de los participantes reales durante la resolución de la tarea. Para ello, se desarrolló un marco probabilístico basado en leyes esenciales del funcionamiento memorístico. El modelo incluía competición entre tasas de olvido heterogéneas, correspondientes a repeticiones sucesivas de cada estímulo. Se simularon participantes virtuales mediante un proceso de Monte Carlo, mientras que la probabilidad de éxito se determinó por ajuste de los umbrales de acierto a los datos experimentales. Los resultados replicaron con éxito el proceso de aprendizaje poblacional de los datos reales, además del rendimiento individual de los grupos favorecidos y controles. Se observó una desviación significativa para el grupo dificultado, que pudo deberse a la influencia de factores externos, como la frustración.

El tercer objetivo fue desarrollar una red neural biológica, inspirada en fenómenos cerebrales relevantes para la compactación del tiempo como la anticipación visual, la precesión de fase theta y la plasticidad sináptica. La red comprendía tres capas que simulaban el proceso de percibir las posiciones iniciales, predecir trayectorias futuras, crear la CIR de la situación y decidir si el estímulo contenía interacciones (colisiones) o no. La red se entrenó mediante competición por inhibición recíproca y aprendizaje supervisado. Los resultados revelaron que las interacciones son fronteras naturales de predicción, en forma de incrementos en los niveles de activación y de respuesta neuronales para ventanas de predicción próximas a las colisiones. Además, las interacciones son eventos que concentran la información del entorno y focalizan la

atención, por lo que son codificadas preferentemente en situaciones de distracción y su aprendizaje es más rápido en escenarios de competición.

En conclusión, este trabajo proporciona evidencias a favor de la representación interna de situaciones dinámicas como abstracciones estáticas o CIRes, organizadas como mapas especiales sin dimensión temporal. La compactación del tiempo es un mecanismo cognitivo preferente en hombres, en contraste con las mujeres, que la utilizan dentro de un abanico más amplio de estrategias. Además, es dependiente del estadio de maduración, actuando como un mecanismo basal pero aún no saliente a partir de los 9 años de edad. La modelización matemática ha demostrado que fenómenos como la consolidación de memoria y el olvido forman parte de su maquinaria cognitiva. Por último, los principios de la compactación del tiempo pueden surgir de forma natural en redes neurales biológicas simples y sin topografía, a partir de mecanismos funcionales preexistentes. La predicción de interacciones se plantea, así, como un elemento mental que estructura procedimientos biológicos básicos de procesamiento de información, como la atención y la memoria.

Abstract

COGNITION AND INTERNAL REPRESENTATION OF DYNAMIC ENVIRONMENTS IN MAMMALS' BRAIN

Time is one of the most prominent dimensions that organize reality. Paradoxically, there are loads of redundant information contained within the temporal features of the natural world, and yet internal coding of time in the brain seems to be crucial for anticipating time-changing, dynamic hazards. Allocating such significant brain resources to process spatiotemporal aspects of complex environments should apparently be incompatible with survival, which requires fast and accurate responses. Nonetheless, animals make decisions under pressure and in narrow time windows. How does the brain achieve this? An effort to resolve the complexity-velocity trade-off led to a hypothesis called *time compaction*, which states the brain does not encode time explicitly but embeds it into space. Theoretically, time compaction can significantly simplify internal representations of the environment and hence ease the brain workload devoted to planning and decision-making. Time compaction also provides an operational framework that aims to explain how perceived and produced dynamic situations are cognitively represented, in the form of spatial predictions or *compact internal representations* (CIRs) that can be stored in memory and be used later on to guide behaviour and generate action. Although successfully

implemented in robots, time compaction still lacked assessment of its biological soundness as an actual cognitive mechanism in the brain.

The first objective of this work was to provide experimental evidence that time compaction is a cognitive strategy present in the human brain. To do so, a sample of 410 participants were engaged in a trial-and-error classification task, particularly designed to modulate learning performance under time compaction assumptions. Participants were prompted to find a hidden association rule between static and dynamic stimuli shown on a computer screen and the up and down arrow keys of the keyboard. According to time compaction, it should be feasible to interfere with the learning process by prior exposition to static scenarios that either matched the CIRs of the dynamic situations or not. As such, associations stored in memory during a first phase comprising static stimuli would favour or hamper the performance during a second phase comprising dynamic stimuli. The results revealed that time compaction is a salient cognitive strategy in men, whose learning rate was modulated as predicted. Women showed no modulation of their learning process, but performed on par with the group of control men. Moreover, women verbalized the rule they found in terms of collisions or future interactions regardless of their performance, whereas only men that quickly solved the task were prone to such verbalizations. This was interpreted as signs that time compaction is a predominant cognitive mechanism in men, whereas women might rely on a broader repertoire of strategies alongside time compaction.

The question of whether or not time compaction has an age onset was also addressed in this work. A sample of 386 children between 8 and 11 years old was collected with that purpose. Children underwent a computer task equivalent to the one described for adults but simpler. The results revealed that time compaction is not yet a salient cognitive mechanism before 11 years of age, although it might already be an incipient strategy acting as baseline in the background, as informed by on par performance between static and dynamic phases, regardless of age and gender.

The second objective was to mathematically simulate the observed behaviour of real participants solving the task. To do so, a probabilistic framework based on basic laws of memory was developed. The model comprised heterogeneity of forgetting rates and competition between memory traces of stimuli’s successive repetitions. Virtual participants were simulated by means of Monte Carlo procedures and success probability was determined by fitting thresholds to the experimental data. The results revealed that the population learning process of real participants can be successfully replicated by probabilistic modelling based on memory.

Individual learning performance of favoured and control groups was also coherent between simulation and observed data, although there was a significant deviation for hampered groups, probably due to the influence of external factors such as tiredness.

The third objective of this work was to develop a biological neural network inspired by brain phenomena functionally relevant for time compaction. Such functions involved preplay activity, theta phase precession and spike-timing dependent plasticity. The network comprised three layers that simulated the process of perceiving the initial positions of moving circles, predicting their future trajectories, creating a CIR for the situation, and deciding whether the stimulus contained interactions (collisions) or not. Decisions were taken under competition by mutual inhibition and reinforced learning. The results revealed that interactions are natural boundaries for predictive effectiveness, evidenced by the increase in activation and neural responses for prediction windows in the vicinity of collisions, and likewise by the decrease beyond the occurrence of collisions. Interactions also act as hotspots of environmental information and organizers of attention, as shown by their salient codification in tasks with distractor elements and by faster learning rates in competitive learning.

Thus, conclusions of the present work include experimental evidence that time-changing situations can be internally represented in the human brain as static abstractions or CIRs, spatially arranged as maps where time is no longer present. Moreover, time compaction is a preferred cognitive strategy in men, in contrast to women, who rely on a wider range of strategies. Time compaction is also dependent on the stage of maturation, and acts as a baseline yet not salient mechanism at least from nine years of age. Mathematical modelling has shown that basic laws of human memory, such as consolidation and competition of memory traces over time, may be involved in the cognitive machinery of time compaction. Lastly, time compaction principles can naturally emerge in a biological neural network, achieved by implementing functional mechanisms ubiquitous in the brain on a topography-free architecture. This revealed that predicted interactions serve as mental anchors that structure basic workflows of biological information, such as forgetting and attentional processes.

Abbreviations

C	Control group
CI	Confidence interval
CIR	Compact internal representation
DM	Dynamic matching stimulus
F	Favoured group
GEE	Generalized estimating equation
GLM	Generalized linear model
H	Hampered group
RF	Receptive field
SCR	Stimulus-response compatibility
SM	Static matching stimulus
STDP	Spike-timing dependent plasticity

1. INTRODUCTION

1.1. Internal representation of the environment

What is environment? Most prominent features: space and time

Defining environment in a cognitive context is a mandatory first step, so everyone can start off a common place. For most people, the word *environment* evokes pictures of dense muddy jungles, dreamy waterfalls under the moonlight, or hot and desert hills of sand. It's not that surprising since most of our everyday exposition to the term has ecological implications, such as "protect the environment", "environment contamination" or "environmental politics" (Anderson, 2013). Thus, although the naturalistic point of view is indeed an instance of the environment, it's not what will be referred in this work, but a more general interpretation.

Intuitively, a broader notion of *environment* involves anything surrounding a system or an organism and the external forces that have a direct influence on that organism' behaviour (Harvey & Hallet, 1977). Following that definition, it might be tempting to try to establish precise boundaries to the surroundings that affect a given individual. Whereas the starting point of the environment could be naturally found where an individual leaves off (i.e. the skin of an animal), its ending point is not that obvious. Do the surroundings include all of the Solar System, distant circumstances that have impact from afar (i.e. via news or phone), or just the place one lives in? Taking into account that the environment doesn't necessarily have a defined metric, the measure of its extent will ultimately depend on the research question at hand (Wachs & Plomin, 1991).

For the scope of the present work, *environment* should be interpreted as the sum of conditions that physically surrounds an organism at a given point of time and space. Restricting to the proximal vicinity allows for measuring whether there are any agencies imposed to the organism by the environment, in virtue of which any changes in its behavioural patterns could be deemed as adaptive reactions. This implies a positivist theory of the environment (Zimring & Dalton, 2003), which entails that it is possible to characterize features, dynamics or other attributes of the environment acknowledgeable by a cognitive agent when deciding for a particular course of action.

Two are the foundational features that organize any given environment: space and time. Note that both have already been mentioned in the definition provided before. All organisms are bounded to act within a three-dimensional space comprised of constantly interacting systems, which in turn are collectively interlinked through causal cascades of events developed throughout time. Nonetheless, the temporal feature of the environment can only be experienced, not altered. Whereas a cognitive agent might be able to reconfigure its physical environment to suit its goals better, it cannot manipulate time. This striking difference between spatial and temporal dimensions introduces a whole new level of complexity that an organism has to deal with, as all decisions and actions must occur not only in space but also in a forward directionality imposed by time.

There is a third component vital to understand how an organism makes sense out of the spatio-temporal attributes of its environment, that is *information*. Although there are several technical definitions for *information* in various scientific fields (Oppenheim et al., 2003), in a cognitive context it is often useful to resort to a more practical meaning. To this purpose, anything in the environment that helps reduce uncertainty so a cognitive agent can make better predictions about outcomes makes the cut as *information* (Rosenfield et al., 2015). Information is such an integral part of the environment that its gathering, processing and interpretation, oriented towards prediction of future states, has been posed as the ultimate force driving the nervous system’s functions and evolution (Llinás, 2001).

Thus, information exchange is at the core of the relationship between cognitive beings and the natural world (Dall et al., 2005). Among the animal kingdom, the human brain seems to be particularly skilful at extracting and using environmental information to foster innovative interactions with its surroundings. There must be then some sort of internal space where the brain represents and structures whichever sources of information are available in the environment, in a way that is spatiotemporally coherent and consistent enough to allow for the generation of policies that drive real time behaviour.

Does the brain make a representation of its surroundings? Mental representations and embodied cognition

The idea that forming internal representations of the outside world is a capability of the brain traces back at least to the first Greek philosophers, who stated that propositional attitudes such as beliefs and desires were in fact intentionality pointers to real things (Pitt, 2004). With the emergence of computational frameworks in the second half of the twentieth century, a

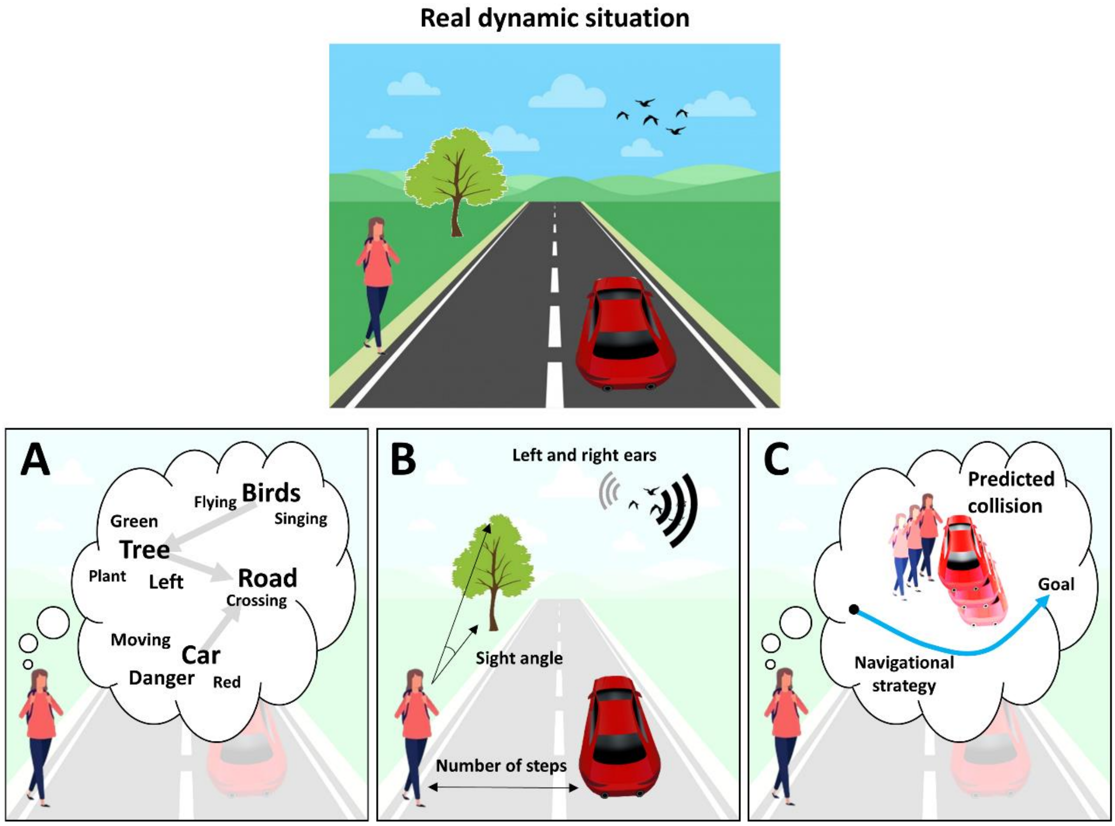

Figure 1. Models of brain-environment interaction. A Mental representation schema. External reality is coded into internal symbols that account for explicit entities, together with specifications of relationships within the system. Mental imagery includes intentions and things that are not present to the senses (e.g. crossing, danger) and may involve any of the sensory modalities (e.g. sight-green, hearing-singing). **B** Embodied Cognition schema. Physical traits of the body constitute cognitive processes by themselves (e.g. head inclination, differential reaching of birds' singing to left and right ears), so there is no representational mediation between brain and environment. **C** Action-based internal representation schema. Both actions and anticipated events share the same representational space. Behaviour can be directly derived from the interplay between prospection and goal attainability.

'representational theory of the mind' equating mental states and cognitive events to computations made by elementary parts of the brain quickly became one of the cornerstones in cognitive science (Field, 1978; Freyd, 1987). Yet to this day, the interpretation of what a *mental representation* is remains rather ambiguous and waves back and forth to accommodate the cognitive model that is most thriving among the scientific community (Clapin, 2002; Issajeva, 2019; Searle, 1990; Van Gelder, 1995).

A barebones notion of *representation* would refer to it as an information-bearing structure that makes the physical world apprehensible to a cognitive agent (Stich, 1992). These representations might start as reactions to external stimuli, that trigger the internal process of encoding something outside the brain into its own domain. In this sense, mental representations are usually deemed as mediators between the mind and the environment (Clapin, 2002; Ramsey 2007). Mental representations have been explained from functional and causal perspectives, which consider objects are represented by its functional role in the environment, according to laws and dependencies governing which external features are encoded (Fig. 1A) (Fodor, 1990; Kriegel, 2013; Loar, 1981). Mental representations preserve biological coherence thanks to the relationship often found between real world events and stable patterns of neuronal activity, which informs about the brain's capacity of developing inner states that coordinate an internal model of reality with its represented counterpart (Issajeva, 2019; Ramos, 2014).

Contrary to the representational approach, the *embodied cognition* paradigm argues against the need of a mental representation that mediates between an organism and the environment (Fig. 1B). Voices in the late nineteenth century were already posing challenges to the separation of body and mind widespread by Plato and Descartes (James, 1890). For cognition to be *embodied*, one must consider that an agent's body features have a significant and physically constitutive role in cognitive processes, lessening the brain's role as a processing machine that needs its own symbolic code to understand the external world, because cognition is sealed away within it (Wilson & Foglia, 2017). In this sense, physical features such as interocular separation or distance between ears can be interpreted as symbols per se that render additional codes unnecessary. Radical *embodiment* rejects the existence of representations and the computational explanation of cognition, as it assumes that an organism's body constitutes a cognitive process in itself (Chemero, 2011; Jacob, 2016). These so-called direct contact theories vary in range, from an enactivist perspective that starts from the individual and its self-regulating behaviour (Schmidt 1988), to an ecological approach that considers behaviour constrained by environmental properties that limit action possibilities (Reed 1988, Warren 1988). Nonetheless, this denial of representations as constructs needed to explain decision-making also has its share of detractors (Schulz, 2018).

In the present work, a moderate middle point between pure representational and basal embodied cognition will be followed (Raab & Araújo, 2019) (Fig. 1C). This is achieved by considering the organism-environment system from an *action-based approach* (Dempsey & Shani, 2015), in which internal representations are not only shaped by actions but also enriched in prospective regulations of events, instantiated at the neuronal level (Hommel, 2015). The main gist of this perspective consists in linking actions and perceptions through a common code, so perceptions can be internally mapped as actions, and anticipation of action goals can directly guide and influence behaviour in return (Mechsner, 2004; Prinz 2013). The common coding principle plays a pivotal role to understand how internal representations are cost-effective solutions to decision making, and will be profusely referred later on in this manuscript to accommodate both spatiotemporal features of environment and cognitive agent's prospections within a common action-based representational space.

What constitutes an internal representation? Theory of event coding

There are some particularities on the nature of action-based internal representations that are worth stressing out. First, note that internal representations are not carbon-copies of the physical world. Despite being directed towards external objects and events, internal representations are by-products of the mind composed by many other elements than those that are being directly fed to the senses (Godfrey-Smith, 2006). Representations' meaning exceeds that of the neurobiological correspondence established by the brain-environment system, as the evoked mental imagery might have not been experienced before (Sternberg & Ben-Zeev, 2001).

Second, for a mental entity to be considered as an internal representation, four minimal features are required (Hubbard, 2007; Markman, 2012): (i) a represented world; (ii) a representing world; (iii) representing relations; and (iv) cognitive processes. Whereas the first three suffice to account for any given representational system, the fourth adds functionality by including procedures as a necessary dimension. These procedures act as decision making policies and have effects on the representing world by manipulating hidden information within the representation's semantics (Gallistel, 2001), allowing the emergence of higher-order cognitive abilities.

A third important assumption underlying action-based internal representations is that they are referred to distal but not proximal aspects of represented events (Prinz, 1992). A good proxy to this notion can be borrowed from the 'theory of event coding' and its layered approach to describe how objects' attributes are experienced internally (Brunswick, 1944; Hommel, 2001). These layers start in the outside world and accounts for the transformation of information modality that occurs as the abstraction of the representation increases (Fig. 2). Extending the logic to an action example, a distal feature might consist in the real distance a foot has to travel to hit a ball, that should match with the perceived distance between the foot and the ball before starting the movement. The proximal event codification would consist in the neural firing pattern representing the distance in the visual system and its synchronization with firing rates accounting for the estimated travel distance in the motor cortex. This drastic change in information modality between distal and proximal codes implies that for an effective communication between perception and action to occur, its common representation should

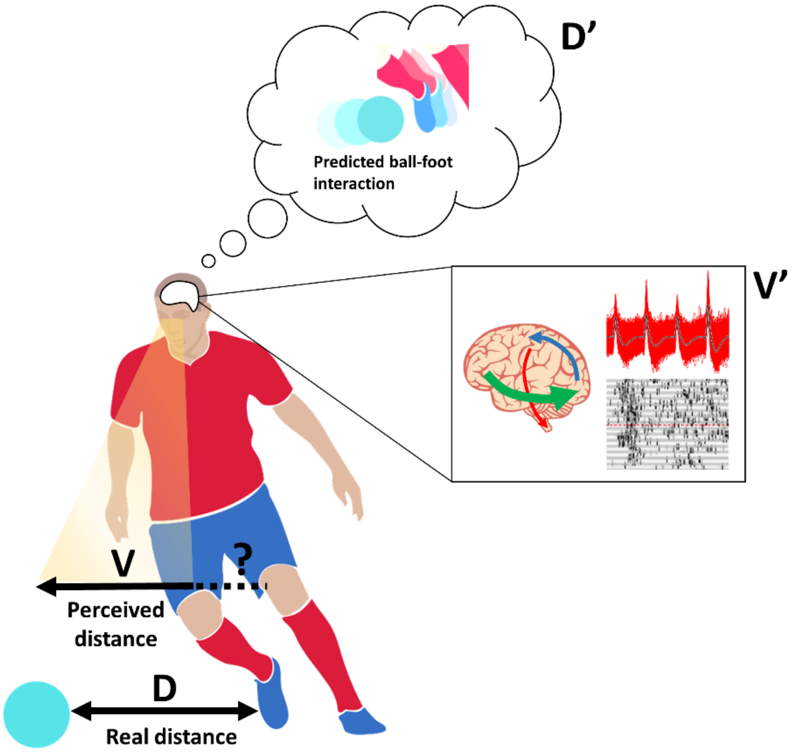

Figure 2. Layering in theory of event coding. Layers are named after D, V, V’ and D’, following the author’s original convention (Brunswik, 1944). Within this framework, any event susceptible of being perceived necessarily has a distal and a proximal representation in the environment (D and V, respectively) and internal representations that point to these external representations (D’ and V’, respectively). Examining how the information flows from one layer to the next is the determinant aspect of this approach. Starting with the most external layer D, its relationship with V is not invariant but depends on the medium (i.e. environmental noise), thus rendering V an incomplete copy of D that can only provide cues but not exhaustive representations of real world events. V’ relation to V relies on physical and biological processes, so it is considered to be direct and invariant as long as sense organs function normally. D’ relates to V’ to the same degree of incompleteness that V accounts for D. Nonetheless, despite the loss of correspondences along the perceptual process, D’ usually ends up being a description of D faithful enough to allow for complex and successful interactions with the environment.

involve features of the external world, not features of the codes that translate them. That is, internal representations are composed of distal features of events akin to the external

environmental qualities, not proximal features of neural pathways. Additionally, the ‘theory of event coding’ provides an extensive framework that will be referred later on in this manuscript to explain how internal representations help guide decision-making.

As a summary of the conditions mentioned above, one could consider internal representations as fundamental blocks of cognition, exploited by organisms to solve tasks and to adapt behaviour (Issajeva, 2019). Internal representations are thus mental entities that transfer information about the physical environment to a separated but functionally related internal domain, that holds some corresponding relation with the external world and its organizational features via the combination of the organism' body and its goals

1.2. Biological significance of internal representations

Which brain structures are involved in internal representations? Role of hippocampus and prefrontal cortex

The cognitive processing of external reality involves distributed networks of brain components, which are gradually recruited. Although the anatomical correlates of internal representations are not well defined yet, it's been extensively argued that their properties emerge as a dynamic property of neural processing between distant but highly connected brain regions. A list of potential candidates would include areas such as the cingulate cortex, temporal gyrus, cuneus, insula and parietal cortex (Jo & Jung, 2016; Mesulam, 1999; Morrison et al., 2011; Shenhav et al., 2013). In this section the focus will be put on the two most studied regions, hippocampus and prefrontal cortex.

One paradigmatic example of brain-environment interactions found in hippocampus comprises movement and orientation in space. As an organism moves around the world, its motor system requires a detailed and stable representation that consistently relates objects in its surroundings to body actions and sensory input coming from sight, hearing and proprioception (Land et al., 2014). In this regard, the term *cognitive map* was first coined to account for highly organized internal representations comprised of external cues and internal states, meant to facilitate rule generalization and flexible interaction with the world (Tolman, 1949). The initial efforts aimed to explain navigational strategies in rodents, who were able to quickly switch to unexplored but more direct paths to a goal after familiar routes were blocked. From these observations arose the idea that animals must have access to spatial knowledge about the environment similar to a map representation, that could be used to guide behaviour. Neurobiological research based on this idea led to the discovery of place cells in the rodent hippocampus, which fire as a function of the spatial position of the animal (Fig. 3A) (OKeefe & Dostrovsky, 1971). Further studies confirmed that place cells' firing fields incorporate allothetic and idiothetic information (Fig. 3B), as they are tuned to the rotation of distant landmarks and can even track location when the spatial cues are removed from the environment (Gothard et al., 2001; OKeefe and Speakman 1987). These observations revealed a persistent encoding of allocentric self-location and a mechanism capable of extrapolating current experience to previously learned maps (Quirk et al, 1990).

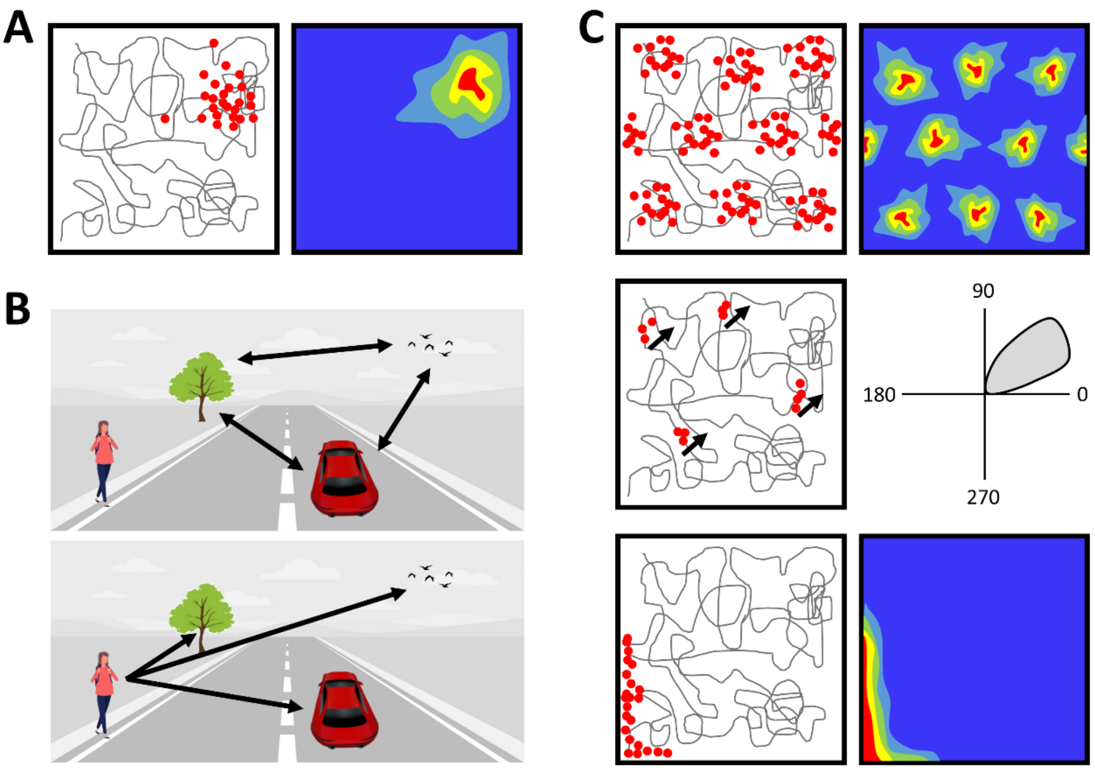

Figure 3. Conceptualization and neural substrates of cognitive maps. A Firing pattern of a hippocampal place cell. Left box depicts the rat's path as the animal wandered in a squared-shaped arena (grey line). Red dots represent positions where the place cell firing rate increased as the rat traversed them. Right box depicts the receptive field of the place cell, with activity ranging from blue (low) to red (high). A place cell sensitive to the top right corner of the arena is shown. **B** Allothetic (top) and idiothetic (bottom) perspectives. Allothetic strategy involves an allocentric point of view, where estimated distances between landmarks or relevant elements in the environment guides behaviour (e.g. navigation). Idiothetic strategy involves an egocentric point of view, where estimated distances from oneself to landmarks are the preferred source of information. **C** Navigational system in entorhinal cortex. Same legend as in A applies here. Top panel: grid cell firing in a regular geometrical pattern. Middle panel: head direction cell firing whenever the rat's head is tilted 45º away from the sagittal plane. Bottom panel: border cell firing whenever the rat approaches the bottom left wall of the arena. A and C adapted from Grieves & Jeffery (2017).

Building on these results, the hippocampal formation quickly became the most plausible candidate to provide a neural instantiation of an internal spatial map. The cognitive map hypothesis has been expanded with subsequent discoveries, revealing additional components of a putative spatial navigation system (Fig. 3C): (i) grid cells in medial entorhinal cortex, which codes metric distances by firing in the vertices of a regular hexagonal pattern of the environment (McNaughton et al, 2006); (ii) head direction cells in cortical and subcortical layers, which tracks the orientation of the animals' head in the navigational plane direction (Taube, 2007); and (iii) border and boundary cells in entorhinal cortex and subiculum, respectively, which fire when the animal is close to limits or obstacles and relates the firing fields of place and grid cells to fixed environmental features (Solstad et al., 2008). Object-vector cells in the hippocampal system have also been recently described (Høydal et al., 2019; Sarel et al., 2017), which simultaneously encode other navigationally relevant quantities, such as distance and direction to physical elements in the immediate vicinity. In conjunction, all these cells provide a multi-layered lattice of position in the nearby environment. However, direct contact has been proven to be not always necessary for hippocampus to form an internal representation of an animal's surroundings. This is evidenced by experiments interrupting the recognition and generalization of geometrical forms shown to rats in inaccessible screens after hippocampal injury (Klement et al., 2010; Levcick et al., 2018), supported by the finding of spatial view cells playing a role akin to typical place cells in monkey's hippocampal formation (Killian et al., 2012).

In contrast, prefrontal cortex has been historically assigned to the maintenance of short-term memories (Goldman-Rakic, 1987). Its characteristic delay-period patterns of activity have often been interpreted as a memory trace, consisting in neuronal activation that follows the transient presentation of an instruction cue and persists until a trigger signal occurs (Constantinidis et al., 2001; Funahashi et al., 1989). Prefrontal cortex function extends beyond memory of recent stimulus to spatial attention, which includes monitoring and selection of information (Rowe et al., 2000). There is a larger proportion of prefrontal cortex neurons devoted to representing attended locations over remembered ones, when both locations are potential targets of saccadic eye movements (Lebedev et al., 2004). This alternative view emphasizes that a top-down control of *attentional selection* or *attention to action* occurs in prefrontal cortex (Rowe & Passingham, 2001). Similar evidence has been found in avian analogous brain structures (Browning et al., 2011; Diekamp et al., 2002). These findings support the idea that prefrontal cortex-like areas might be playing a role in the symbolism of internal representations and stimuli generalization, as rule-guided behaviours are associated with the synchronic functioning of these regions with basal ganglia (Kriete et al., 2012).

A significant commonality between hippocampus and prefrontal cortex is the presence of feedforward and recurrent neural circuits, which are known to be able to realize efficient and universal function approximations (Eldan & Shamir, 2016). These areas express highly conjunctive representation of both valences of stimuli and geometry of the environment. The population code in the hippocampus is hierarchically organized to encode context, position, objects, and their values, both at perceptual and mnemonic levels (McKenzie et al., 2014). Prefrontal cortex contains conjunctive coding as well, but without an apparent hierarchical organization (Rigotti et al., 2010). The representation in these areas can be distinct from the immediate sensory environment or its direct implications for values or actions. Hippocampal CA1 and CA3 exhibit both spontaneous and task-related replay of spatial trajectories during active and passive behavioural states (Carr et al., 2011). In the prefrontal cortex, neurons can persist in their response to a stimulus even after it has disappeared (Mante et al., 2013). Such representations can underpin forms of working memory, allowing information that is no longer present in the environment to affect behaviour.

Thus, it seems plausible that both hippocampus and prefrontal cortex are the kernel areas that guide the cross-talk between brain regions involved in the generation, storage and recovery of internal representations. This paves the way to questioning to what extent internal representations are a valid construct to understand how brained animals generalize behaviour-guiding principles from experience.

Are internal representations ubiquitous among encephalized animals? Evolutionary perspective

The impact of evolution in the generalization ruleset that the brain is able to represent, opens up the question of whether non-human animals make internal representations as complex as the above described, if any. A first approach to this question might rely on observable anatomical differences. For this matter, a preliminary cut-off would leave out any species lacking cephalized nervous structures that could act as a central processing system (i.e. cnidarians, sponges and jellyfish). Later invertebrates such as arthropods cannot be that easily discarded, as they possess brain-like anterior ganglions with various levels of specialization (Striedter, 2005) and are capable of real-time adaptive behaviours elaborated to high degrees (Pahl et al., 2013). Nonetheless, vertebrates should be considered as the elementary template to which the internal representation principles here described can be directly applied. This is due to all of them sharing correlates of the nervous structures previously described as potential candidates, and the existence of a bone-encaged central brain with sophisticated functional distribution (Herculano-Houzel, 2011). Homologue to mammal's hippocampal formation can be found in the medial pallium cortex, which is present in all vertebrates and conserves many of its connections to other brain regions as well as its spatial representation function (Bingman et al., 2009). Strikingly, prefrontal cortex is still lacking a universally acceptable definition, and it is usually regarded as the region of the cortex whose principal thalamic afferences come from the mediodorsal nucleus (Carlén, 2017). This cortical region is located at the anterior end of the cerebral hemispheres in mammals and actually refers to a group of related areas. Although this poses an obstacle to establish homology across vertebrates, it is accepted that prefrontal cortex is greatly expanded in primates, which might account for the apparently deeper cognitive traits they can exert (Briscoe & Ragsdale, 2019; Kuboshima-Amemori & Swaguchi, 2007).

A second approach to examine the prevalence of internal representations in the animal kingdom is behaviour (Ramos, 2014). As stated before, behaviour arises from the covariation of an organism's neural states with changes occurring in the environment, which is the first condition for establishing a representation of any kind. In the past decades there's been a rapid increase in research interest regarding animal's mental representations, mainly focused on mammals' and birds' capabilities for sequential problem-solving (Auersperg et al., 2013; Martín-Ordas & Schumacher, 2012; Sabbatini et al., 2014; Taylor et al., 2009), action planning (Beran et al, 2015; Kabadayi & Osvath, 2017) and complex cognition (Baciadonna et al., 2020). One key question has been the extent to which animals accommodate internal representations through mental trial and error. Such imaginings have clear adaptive value and have been recently found in crows (Gruber et al., 2019), which were able to mentally represent the sub-goals and goals of metatool problems. That way, animals can try out in their head which courses of action might kill them or reduce reproductive chances, and avoid them in the real world. Another famous example of internally generated states is the mirror neurons system, originally found in macaque monkeys (Rizzolatti et al., 1999). These neurons fired in response to the sight of another animal (a conspecific or even the experimenter) performing actions similar to those included in its natural repertoire. Neuroimaging and electrophysiological studies indicate that the mirror neurons system also operates on the basis of pre-prepared structures that serve for action recognition in monkeys, whereas their role in imitation and language might exclusively belong to humans (Oztop et al., 2013).

Nonetheless, the basic constituents to this capacity can be traced back to simpler reactive or conditioned behaviours also present in invertebrates and insects. Even though their representational capabilities might be limited and hardly considered of cognitive nature, it is still an optimized solution to the compromise between physiological constraints and the necessity of gathering and processing sensorial information, in the context of selective pressure in a specific niche (Barron & Klein, 2016). Thus, the construction of a set of accurate and useful representations requires a complementary mechanism of validation and improvement that, in biological organisms, can be implemented by the process of natural selection.

What is the biological relevance of internal representations? Economy of survival

From a biological perspective, the immediate utility of behaviour guided by internal representations is increasing organisms' survival chances in different contexts (Edlund et al., 2011). One of the main enhancements that action-based internal representations provide to information processing relies in the creation of subsets of a priori representations available for use in natural situations. As an example, escape behaviour engages a wide range of processes from simple stimulus reactions (i.e. reflexes) to decision-making and action selection (Qi et al., 2018; Roberts et al., 2011). The flexibility necessary for animals to survive in dynamic environments ultimately comes from the cognitive control of these processes, using memory and quickly deciding between alternative options (i.e. prey escaping from pursuing predators must dynamically compute escape strategies and trajectories) (Cooper et al., 2015; Ellard et al., 2009). For innate capabilities such as threat detection and escape to occur in adequately real time, relevant computations need to be cached and ready to use as pre-existent cognitive constructs, in the form of internal representations that can guide fast prospections (Evans et al., 2019; Mobbs et al., 2020).

It is worth noting that key areas for threat detection and defensive behaviours, such as the superior colliculus and amygdala, are also involved in the control of spatial attention and saliency maps orchestrated from the prefrontal cortex (Krabbe et al., 2018; McGarry & Carter, 2017; Rozeske et al., 2018). The existence of neural substrates tuned for features that characterize threatening looming stimuli probably reflects strong selective pressure for a collision-avoidance system (Blanchard, 2017; McNaughton & Corr, 2004; Schackman & Fox, 2016). This may suggest that threat detection is fundamentally a process that link salient events in sensory space with actions.

Identifying threats and implementing adequate responses is a high velocity process prone to representational errors, mainly due to the distorted simplification of external situations. However, even incomplete or partial representations may improve survival chances, as they are quickly created and corrected in real life situations (Molet et al., 2012). This style of cognitive functioning can be understood as a survival economy trade-off, in which errors of commission (wrongly reacting to a non-threat) are more acceptable than errors of omission (not reacting to a real threat) (Ramos, 2014).

In modern humans, for whom escaping sudden threats is no longer a predominant survival activity, there are other cognitive capacities like empathy and face recognition that also seem to work with pre-prepared representations (Kryklywy et al., 2013; Prochnow et al., 2013; Regenbogen et al., 2012). If cached internal representations pose such importance as to underlie not only survival abilities but also other cognitive functions, analysing how learning and memory work in consonance to provide robust mechanisms for storage and retrieval is a natural next step.

1.3. Cognitive correlates of internal representations

Are internal representations stored in the brain? Role of learning and memory

The extent to which stimulus or action values are updated within internal representations should be sensitive to environmental uncertainty. Following performance of an action, computing the expected outcome requires the integration of signals across highly reciprocally interconnected brain areas (Doya, 2008). This uncertainty network includes the anterior cingulate cortex (Rushworth & Behrens, 2008), basolateral amygdala (Costa et al., 2016), hippocampus (Unal et al., 2015) and mediodorsal thalamus (Mitchell et al., 2007). The internal values that each of these areas represent frequently overlap, which supports the idea that learning involves inherent interactions between expected and unexpected uncertainty signals.

Thus, successful learning requires mechanisms that change behaviour in a substantial manner when an unexpected source of information is found in the external world. This means updating internal models due to signals of environmental volatility but not after expected variability (i.e. robustness to noise). Under stable conditions, uncertainty can be deemed *expected* when it reflects unavoidable and ubiquitous variability, which provides a baseline level of stochasticity against which gains of learning caused by surprising events (i.e. volatility) can be measured (Soltani & Izquierdo, 2019). As such, *unexpected* uncertainty has a strong component of subjective perception due to sudden changes in reward probabilities, magnitudes or delays (Farashahi et al., 2018). However, in practice, organisms face dynamic non-constant environments, where verifying whether event probabilities change or not over time is often not feasible. Learning in such time-changing environments is controlled by a trade-off between adaptability (the ability to respond quickly to changes in the environment) and precision (which requires slower update after each feedback) (Farashahi et al., 2017). One way to reach stability between the two may be to increase the rate of learning after unexpected events and decrease it when the world is stable (Iigaya, 2016), which can be optimized by the retrieval of stored representations.

In this scenario, memory acts not only as a natural consequence of learning, but as an organizer of cognitive elements (Wyer, 2007). Classical associative and reconstructive models of memory offer explanations compatible with behaviour guided by action-based internal representations. In the associative paradigm, internal representations are bodies of knowledge or nodes connected to each other by pathways of variable strength, in a network fashion. The identification of an individual element contained in a representation activates its particular node and the excitation spreads through the network following the strength of associations, either in parallel or sequentially (Kohonen, 2012). Once an element is no longer thought about (deactivated), its corresponding excitation gradually decreases. Still, the element will be more easily accessible as long as some residual excitation exists. This can account for the effects of frequency and recency of thinking about a concept based on its accessibility in memory and, therefore, on the likelihood of generalizing it to a novel situation to which it has potential application (Tan & Ward, 2000).

Reconstructive models complement the associative network explanation by adding a retrieval cue conceptualization. It's been shown that not all of the features of an experience are encoded into memory at the time one encounters it (Leshikar et al., 2012). When the event's representation is later recalled, it is often necessary to fill in gaps by inferring elements that were not contained in the memory representation formed at the time of occurrence. This could be done on the basis of internal representations acquired in similar situations. Features that have been added in the course of reconstruction are indistinguishable from features that had originally been stored (Mori, 2008). A probabilistic top-down search is then performed when a particular knowledge needs to be used for the objective at hand, and a copy of the representation is retrieved and placed in working memory. A notable example can be found in the Stroop effect (Kiyonaga & Egner, 2014; Stroop, 1935), which implies that content in working memory should affect behaviour to the same extent as an externally attended and perceived stimulus would (Fig. 4). This supports the idea that working memory and attention operate on the same representations and rely on similar resources. Thus, the identification of goal-relevant internal representations is a workflow of processes similar to those assumed by models of cue retrieval.

Various types of representations have been postulated to exist in memory. They can be coded verbally, visually or in other modalities (Mayer, 1994; Péran et al., 2010). They may be episodic and semantic knowledge representations (Patterson et al., 2007), or pertain to phenomena attributed to declarative or procedural knowledge processing (Pezzulo, 2011). Their features may also be temporally or spatially constrained or have no particular relationship except for their coincidental occurrence within a reference timeframe. From here, it is possible to separate categorical representations, whose elements have no a priori relatedness, from schematic representations, whose features are causally organized according to verifiable spatial or temporal rules (McNamara, 1986; Astle et al., 2012). The latter distinction will be of particular utility in the present context, as it is possible to evaluate what is the impact of different mental policies and models in the computation of internal representations whose features are constrained by physical attributes of the environment.

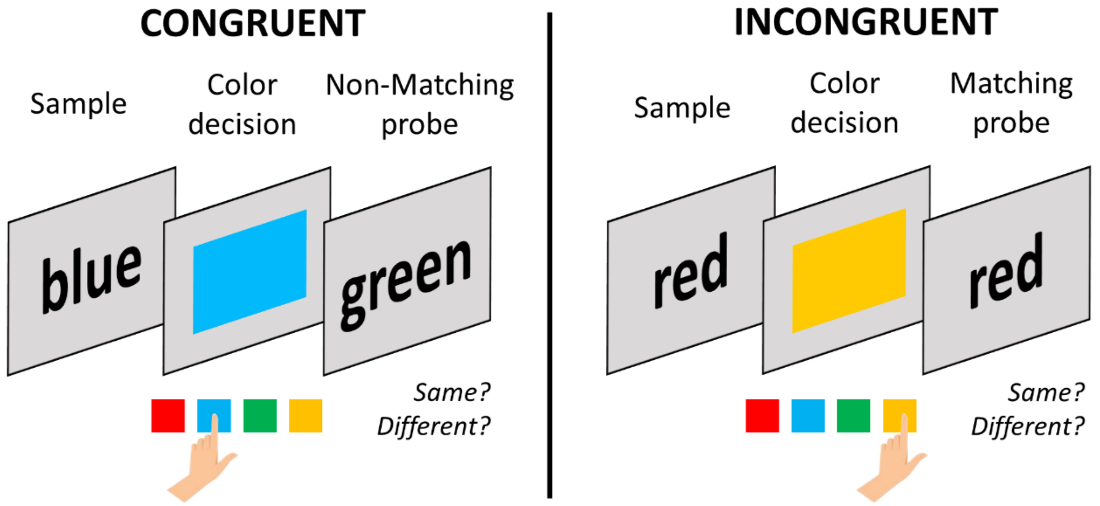

Figure 4. Effect of memory and attentional interference on behaviour. In the example task, participants were asked to remember a word (sample) and then indicate which was the filling color of a rectangle. Afterwards, they had to report whether a probe word matched the previous sample, stored in working memory. On congruent trials, the colored rectangle (attention) and the meaning of the sample (working memory) agreed (blue-blue), whereas on incongruent trials, they differed (red-yellow). Probe words could match the sample word or not. Performance was poorer in incongruent trials in terms of average number of successes due to attentional interference on working memory. Adapted from Kiyonaga & Egner (2014).

Are there any generating policies of internal representations? Model based and model free prospection

The acquisition of information and creation of internal representations has been proposed to occur in a two-step process. First, it is necessary to have a sufficiently complex brain structure capable of generating internal states that co-vary with external events (Ramos, 2011). Second, the validity of these representations must be measured by contextualization within the environment, which can be considered as part of the process of ascribing meaning to the collected information. It is noteworthy that the generation of internal representations is typically a by-product of ongoing processing workflows, not itself a goal of information processing (Wyer, 2007). This goes in line with a parsimony principle, which implies that internal representations are no more complex than the requirements of the processing objective they are supporting. As such, cognitive constructs usually associated with the concept of internal representation are combinations of simple interactive behaviours (i.e. chaining predictions of future collisions, path planning and procedural knowledge to carry out a certain task) (Cartmill et al., 2012).

Therefore, generating policies of internal representations cannot be isolated from its naturalistic context, where they are meant to facilitate prospective planning of future reactive executions. Following the imminence continuum model (Fanselow & Lester, 1988), different methods of planning can be ascribed to different spatiotemporal scales, exemplified by two extreme policies: surprising or proximal actions will reduce decision space and utilize *model-free* architectures, while distant decision allow increased information processing supported by *model-based* operations. Model-free and model-based computations are often intertwined, particularly under conditions of safety, and have direct consequences over mechanisms of learning, estimation and prediction (Haith & Krakauer, 2013).

Model-based (or goal-directed) computations reflect prospective simulation of the tree of possible future actions and outcomes. These computations are slow but can accurately represent all of the information available to the organism (Doya et al., 2002). Model-free (or habitual) choice is simpler and faster, reflecting instead learning from previous real or simulated experience (Degris et al., 2012). This requires substantial learning to be accurate, because it works by a bootstrapping process that can be particularly challenging given the life-threatening cost of collecting information and the heterogeneity of situations where survival might be a priority (Blanchard et al., 2011). Fortunately, even partially accurate model-free outputs can be helpful, as the bootstrap enforces consistency between successive estimates, creating a response analogous to a reflex that leads to unexpected increases in predictive value. Let consider a basketball match as an example. Prior to the beginning of the match, the coach plans a strategy that involves multiple interactions and solutions to situations that might happen in the court. In other words, the coach follows a model-based approach, as no urgency is imposed and all possibilities and alternatives can be fully explored. Nonetheless, once the match starts, players are left on their own to take decision in the heat of the game. Even though there was an initial model (plan), players will resort to model-free strategies to take quick decisions in real time, which will yield better results the more experienced the player is and the more learned resources can be fed to the bootstrapping process.

Mixed approaches suggest that internal models of the environment can generate simulated observations that recapitulate what the organism might actually experience (Krueger & Griffiths, 2018). For instance, various algorithms replace distal parts of the prospective simulation tree that would normally be used to evaluate future states in a model-base manner with model-free estimates of intermediate values. Since model-free control is faster than model-base, there is particular advantage in training it offline to make it accurate. Sample generation, which can also be seen as a form of scenario testing, can credibly operate only offline, when model-based and model-free systems are not engaged in controlling real time behaviour. This allows exploration of virtual failure or success without exposing itself to the risky consequences of testing it out in the real world (Frank et al., 2013). Following the basketball example, the team could try out tricky situations that could potentially arise in the court. That would be the equivalent to an offline training of a model-free approach: if the coach's plan is the exhaustive model-based exploration of the tree of possible strategies, it's feasible to prune the leafs leading to dangerous situations by practising and acquiring experience that will improve the model-free decisions taken in the heat of the real match.

The representation in the brain of policy-generating algorithms involves large and distributed populations of neurons. The substrates of model-based control in general include regions of the prefrontal cortex, the hippocampus, and the amygdala (Bornstein & Daw, 2013). As noted above, a mixture of model-based and model-free mechanisms are likely to be involved in situations where a threat is present. For example, many animals will exhibit pre-encounter behavioural patterns when a threat arises, yet will switch from model-based planning to model-free calculations as it nears (Moscarello & Maren, 2018). The switch from model-based to model-free may also be reflected at the level of the prefrontal cortex and hippocampus. These regions can drive the same defensive behaviours through different pathways (Do-Monte et al., 2015).

Then, a common goal of these policies is generating internal representations that support the emergence of another property of cognitive systems: anticipating future events. Internal representations are anticipatory in nature, emerge through experience and regulate behaviour through prospection of action effects. In particular, anticipations stemming from internal representations serve two purposes that will be addressed in the next section: selecting appropriate actions and evaluation of action outcomes in the context of a particular goal.

Can internal representations drive behaviour? Mapping actions and decision making

Representational decision-making relies on the aforementioned event coding, by which perception and action share a "common code" and thus are represented together. This implies there is a bidirectional influence between judgement and decision-making, as the action dynamics constrains the array of potential decisions incorporated into the internal representation (Lepora & Pezzulo, 2015). Selection and programming of an action are assumed to represent two distinct but sequential stages, with selection being the most capacity demanding. Selecting an action comprises choosing an abstract symbol representing the appropriate action, whereas action programming can be conceived of as translating that symbol into a program that can actually be performed.

Alongside the functional role of mental planning and anticipation of perceptual effects, current perspectives focus on the goal-directedness property of structured cognitive representations of action effects (Gentsch et al., 2016). For skilful coordination to happen, appropriate internal representations of the motor task and action goals need to be constructed, given that outcome of a decision is often uncertain and can vary over repeated trials (Schack & Mechsner, 2006). In this sense, the existence of so-called *basic action concepts* has been supported from research in sports and cognitive psychology fields (Maycock et al., 2010, Schack & Ritter, 2013; Tenenbaum & Land, 2009). Analogous to the classical term of *basic object concepts* (Rosch, 1978), *action concepts* are the cognitive counterparts that represent elementary body postures and movements directed to achieve a certain action goal, and as such refer to properties of movements that are better described through proprioception. According to the cognitive action architecture approach (Schack et al., 2014), internal representations are built on top of basic action concepts, and their structural composition in relation to one another.

In this sense, the ‘theory of event coding’ offers a comprehensive collection of most of the principles governing the link between internal representations and decision making (Hommel, 2019). Actions are cognitively represented by codes of their perceptual consequences, so perception is not something solely imposed by a stimulus but the very experience of performing an action. For example, saccadic eye movements not only respond to stimuli gazing but also create new information on the retina, and hearing or tactile perception is performed by orienting the head and body towards the source of stimuli. Perception is just as well the consequence of action as it is its cause, which emphasizes the notion that perceptions and actions are internally represented in the same way.

This ideomotor approach to the representation of stimulus and action events and the way these representations are controlled explain various phenomena related to the stimulus-response compatibility effect (Brass et al., 2000; Kornblum et al., 1990). Compatibility effects are commonly attributed to the similarity between features of stimuli and responses, which affects behaviour by biasing the response in favour of the overlapped stimulus feature (Fig. 5). Common event coding provides a robust solution to this concern: given that perception and action-based internal representations are literally related to the same neural codes, whether these functions are meant to represent the stimulus or the response is no longer an issue and does not have further implications for the way the event is represented (Hommel, 2009).

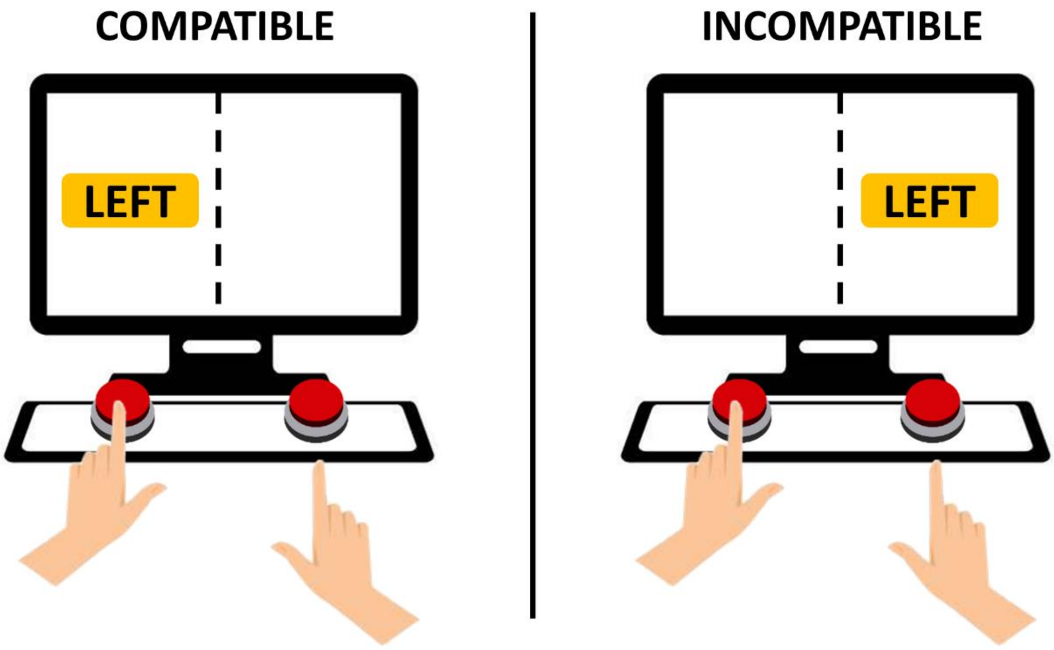

Figure 5. Stimulus-response compatibility effect. In the example task, the participant had to press the left button (response) whenever a “left” prompt appeared on the screen (stimulus). A trial is deemed compatible if the stimulus position on the screen corresponds to the response button (left-left), otherwise, the trial is incompatible (right-left). Average response time was higher for incompatible trials due to conflict between features shared by both response and stimulus, in this case, position or laterality. Adapted from Stoet (2017).

Intentional weighting is an additional mechanism provided by event coding to account for the impact of internal representations on performance (Memelink & Hommel, 2013). The assumption is that getting ready for a task involves the priming of task-relevant dimensions, such as colour, shape, or higher order perceptual or semantic features. Such priming increases the impact that features being coded on it have on object selection and performance. One example for how this mechanism works comes from two-dimensional Simon tasks (Fagioli et al., 2007; Rubichi et al., 2005), which interleaved horizontal and vertical stimulus-response compatibility effects with another task that required either horizontal or vertical stimulus coding. The second task strongly biased performance of the first one by increasing compatibility effects on the direction it made salient and decreasing compatibility effects on the other one.

In summary, the role of internal representations in decision-making is to guide action selection by integrating response patterns with relevant perceptual codes of to-be-expected effects, according to ideomotor paradigms such as event coding. This enables a robust evaluation of the success of the action once it is executed. Then, if it’s possible to obtain a cost function of action-based internal representations, computational modelling of action control should also be feasible. The next section will tackle what assumptions are usually made to translate the biological complexity of cognitive phenomena to discrete mathematical constructs, which starts off by quantifying the degree of discrepancy between expected action effects and actually generated behaviours.

1.4. Computational models of behaviour.

Can statistics explain learning under uncertainty in dynamic environments? Behavioural models

It is often useful to resort to probabilistic framework to properly describe phenomena at population level. In statistical models of learning, an ideal observer would use the Bayes rule to optimally update and estimate the probability of reward or other important quantities (Behrens et al., 2007; Nassar et al., 2010). Under this assumption, the decision-maker or learner establishes a working model of the environment and determines which regularities are expected to change over time, adjusting the parameters of the model on the basis of reward feedback (Courville et al., 2006). Parameters of Bayesian models could represent different properties of the environment such as the probability of reward (expected uncertainty) or the temporal dependence that any of the underlying parameters may have (unexpected uncertainty) (Payzan-LeNestour & Bossaerts, 2011). Therefore, probabilistic models estimate not only stimulus values or action success, but also different sources of uncertainty associated with those values.

Although quite generalizable, the computations required in models of behaviour cannot easily be mapped to neural processes. Moreover, because probabilistic models are mainly focused on describing optimal scenarios, they are somewhat limited in accounting for real choice and learning behaviours in dynamic environments (McGuire et al., 2014). One approach to overcome these issues consists in incorporating additional components to the model, such as explicit forgetting and learning rates (Funamizu et al., 2012), so that the effects of known uncertainty sources can be estimated.

Classic models of learning based on internal representations assume fixed learning rates (Sutton & Barto, 2018). Adding reward prediction errors to the model opens up the possibility to adjust learning rates for each stimulus based on how unexpected the last outcome was, such that surprising reinforcement (or non-reinforcement) results in increased success rate and faster learning (Diederen & Schultz, 2015). In these cases, reward expectancy can be used to control the gain of learning, factoring surprise as a function of either the mean value or the variance of reward prediction errors (Faraji et al., 2018).

Developing sub-optimal approximations is another strategy that can provide better fits to behaviour and links to potential neural substrates. For example, mixture models of human performance are able to surpass optimal Bayesian models on predictive-inference tasks just by updating error rules as a difference between estimated outcomes and actual behaviours (Wilson et al., 2013). Ideal observer models are related approximations to these error-driven rules that adjust the influence of newly experienced outcomes as a function of ongoing estimates of expected uncertainty and drastic changes in the environment (Nassar et al., 2010). These approximate models tend to provide good fits to behavioural data for continuous reward feedback and have been used to identify neural correlates of belief updating (Vossel et al., 2014).

Can neural processes of rule learning and decision-making be simulated? Neuronal models

Neuronal models aim to explain how internal computations are performed by neural elements. Functional networks replicating actual neurons' biology comprise the core component of these simulations, making the mapping onto brain circuits and substrates more feasible than in the Bayesian models outlined above. Although modern depictions share a basic corpus of physical and chemical laws that govern the electrical properties of neuronal transmission, there is a plethora of models that differ in the insight to which the mechanistic aspects of the cell are described. A brief enumeration of the most impactful ones would include electrical input-output models (i.e. integrate-and-fire) (Hodgkin & Huxley, 1952; Izhikevich, 2003; Naud et al., 2008), stochastic models of voltage and spike timing (Galves & Löcherbach, 2013; Gerstner & van Hemmem, 1992), sensory input-stimulus encoding models (Nossenson & Messer, 2012; Siebert, 1970) and pharmacological models (Cui et al., 2017; Koch & Segev, 1998). The coexistence of such a variety of descriptive models for different levels of detail is a side-effect to the need of accommodating scalable experimental setups, a prevalent issue in neuroscience that arises from the difficulty of isolating properties of single neurons from network and measurement effects (Gerstner et al., 2014).

Despite neuron modelling being an important factor in the explicability power of a model, the defining factor in simulations of decision-making behaviour relies on the chosen network architecture and the biological principles underneath. Drift diffusion models that assume differential integration of information over time have been widely used in modelling two-alternative choice tasks (Ratcliff, 1978). In this kind of models, the system comes to a decision when the accumulated difference favouring each choice reaches a certain threshold, which is enough to explain the characteristic trade-off between accuracy and response time in behavioural experiments (Ratcliff & Rouder, 1998). Probabilistic self-excitatory circuits comprising pools of both excitatory and inhibitory spiking neurons have been built on top of the drift diffusion formulation (Wang, 2002). Mutual inhibition mediated by intermediate neurons allows for competition between two decision-making nodes, acting as accumulators of membrane potential instead of information difference. The accumulator that wins the competitions keeps firing, which stablishes a natural link between phenomenological decision-making and the biophysical level. However, rewarding or punishing feedbacks are not implemented in these models, as they assume that the decision has been already learned (Wei & Bu, 2017). Then, real experiments based on force choice-tasks cannot be fully reflected here, as laboratory animals typically undergo a training phase before a stable performance is reached.

Synaptic plasticity is the foremost mechanism that enables reinforcement learning in a neuronal model. Even simplified spike-timing dependent plasticity (STDP) allows to adjust synapse connections on a trial-by-trial basis (Markram et al., 1997). Each time presynaptic or postsynaptic neurons fire, synaptic strength is recalculated and modulated to a desired learning intensity, decided by parameters such as decay rate and refractory period (Lisman & Spruston, 2010). Timing between pre- and post-synaptic firings is then used to code whether synaptic potentiation or depression occurs. For example, the connection between two neurons is potentiated only when the presynaptic spike precedes the postsynaptic by a few milliseconds, whereas earlier or later timing mismatches lead to connection depression.

Models of learning processes also benefit from mimicking functional phenomena governing areas such as hippocampus, prefrontal cortex or amygdala, which have been already mentioned as playing relevant roles in representing environmental uncertainty (Soltani & Izquierdo, 2019). Particularly, recurrent network models of spiking neurons based on hippocampal region CA3 and feedforward networks from region CA1 have been extensively used to explore the dynamics of storage and recall (Graham et al., 2010). Associative memory storage works on the basis of connections' strengthening between coactive neurons, so recall may happen by cueing activity across neurons even after partial matching with previously stored patterns (Vicente & Amit, 1989). In addition, hippocampal theta rhythm (4-7 Hz) ensures that appropriate firing thresholds are set on each neuron that receives input from layers of already active neurons, in an heteroassociative manner (Hasselmo & Fehlau, 2001). Pacing imposed by theta rhythm oscillations from septum GABAergic neurons to hippocampus has been shown to split memory formation into two half-cycles, functionally related to encoding and retrieval of memories, respectively (Hasselmo et al., 2002). Hippocampus-like networks have also inspired neuronal models for efficient parallel mental exploration of alternatives in navigation, where synaptic connectivity is altered by propagating waves of spiking neural activity (Ponulak & Hopfield, 2013). This generates vector fields of local synaptic changes that allow one-shot learning of optimal solutions to reach selected targets.

Thus, learning and retrieval of internal representations is an emergent property of models built on top of wave propagating neural circuits with spike-timing dependent depression/potentiation. Nonetheless, applying these principles to dynamic environments should add prohibitive levels of complexity to internal computations, which so far hasn't been described as an actual issue limiting real time behaviour.

1.5. Compact Internal Representations

How are time and space internally represented? Evidences for spatiotemporal entanglement

Characterising how and to what extent the spatiotemporal dimensions of the environment translates into its internal representation has led to intense development of experimental research mixing cognitive psychology and neurobiology (Buzsáki et al., 2014). Growing experimental evidence suggests that brain mechanisms devoted to spatial cognition may also be involved in the processing of temporal information. Summarizing direct antecedents already mentioned in this manuscript so far, neural bases and their cognitive correlates for processing static (i.e., time-invariant) situations are reasonably well established in the form of spatially selective neurons in hippocampus (Epstein et al., 2017; Fyhn et al., 2004; O'Keefe, 1976). At the population level, phase precession enables the encoding of compressed temporal sequences of animal's past locations in the timing of place cells' firing (Fig. 6) (Jeewajee et al., 2014; O'Keefe & Recce, 1993; Skaggs et al., 1996). Moreover, these neurons are also capable of integrative processing of space and time, since some of them exhibit predictive planning activity in path integration and can even behave as time cells (Eichenbaum, 2014; Kraus et al., 2015). Given the apparent deep entanglement existent between time and space in critical neural processes, a relevant question is how could this work at the functional level.

To this day, there is little knowledge on the mechanisms underlying cognitive processing of dynamic (i.e., time-changing) situations. An exemplary process is mental navigation, which involves imagining a sequence of possible future states (Brown et al., 2016; Johnson & Redish, 2007). The notion that thinking is like navigation roots in the internal construction of scenes, understood as spatial frames populated with meaningful content that can be used to evaluate possible consequences of behaviour (Buckner, 2010; Epstein et al., 2017). This proposition has been supported by the recent identification of path planning adaptive temporal mechanisms, mediated by prospection of combined spatial representations (Arnold et al., 2016). The interplay between time and space is also particularly prominent in memory, where they act as crucial

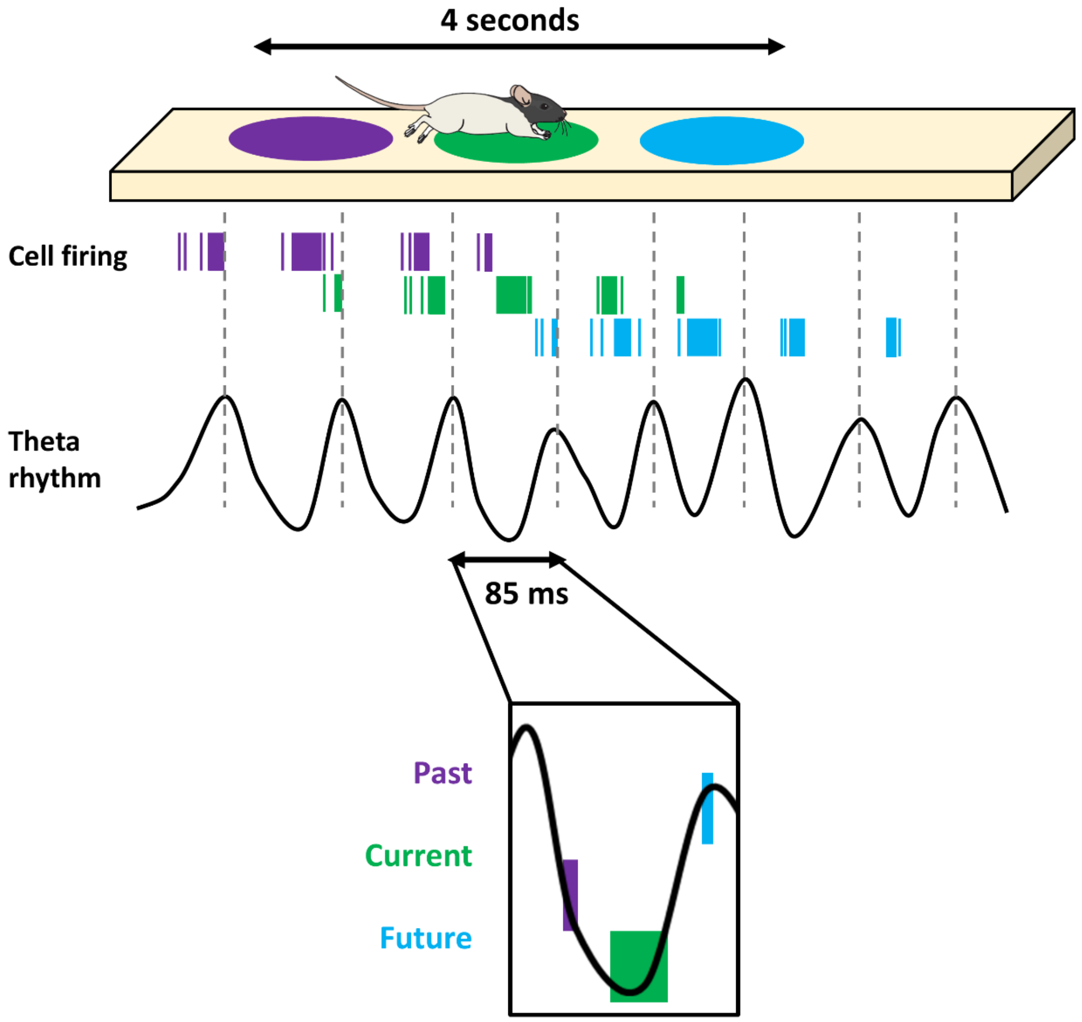

Figure 6. Theta phase precession. Hippocampal cells fire as a rat traverses a linear track and moves through the cells' receptive fields (coloured ellipses). Firing rates act as a code for location and also as a temporal one, as spike trains (vertical coloured bars) occur at successively earlier phases of the theta rhythm. This phenomenon is named after theta phase precession. Spatial sequences of place cells can be represented temporally within a theta cycle, so for the animal's current position, the theta cycle contains information about past, present and future locations. Then, theta sequences anticipate behaviour ahead of time and temporally compress spatial information (4 seconds of real time behaviour coded in a theta sequence of 85 ms). Adapted from Poulter et al. (2018).

contexts for binding declarative object representation to support procedural cued recalls (Manohar et al., 2017). All these converging evidence leads to the conclusion that one of the critical areas shaping cognition, the hippocampus, might be involved in the general structuring of spatiotemporal experiences, far beyond the mere spatial domain, the function widely ascribed to it nowadays (Quiroga, 2019; Rueckemann & Buffalo, 2017). Thus, it may be possible to suggest that representations of space and time in the brain, far from being independent processes, are notably interweaved.

Paradoxically, despite the massive amounts of redundant information contained within the temporal dimension (Bubic et al., 2010), coding of time seems to be mandatory for anticipating complex dynamic, time-changing hazards (Kraus et al., 2013; Livesey et al., 2007; Rao et al., 2001). Devoting such significant brain resources to processing spatiotemporal features of the environment should apparently impede the kind of fast and accurate responses required for survival, and still, animals are able to make decisions in narrow time windows. How does the brain achieve this?

An effort to resolve the complexity-velocity conflict led to a theoretical hypothesis called *time compaction* (Villacorta-Atienza et al., 2010), which states the brain does not encode time explicitly but embeds it into space. Theoretically, time compaction can significantly decrease the complexity of internal representations and hence reduce brain resources involved in trajectory planning, e.g., when moving in a crowd (Villacorta-Atienza et al., 2015). It also provides a natural basis to the cognitive processing of dynamic situations and serves as a building block for constructing episodic memory (Villacorta-Atienza & Makarov, 2013). Therefore, time compaction is a general framework that aims to explain how time-changing perceived and produced events are cognitively represented, in the form of purely spatial interactions that can be used to guide behaviour and generate action.

What is the theoretical framework of time compaction? Time represented as space

Static situations (e.g., a room with furniture or a maze) can be extremely complicated by themselves, as described by the position of multiple objects, their shapes, colours or textures. Time-evolving scenarios further amplify this complexity, with the additional uncertainty of how much will last the events affecting oneself. This constraint has dramatic consequences when the organism's survival depends on making fast and reliable decisions in situations of environmental urgency (fighting, hunting, escaping, etc.). Then, it seems highly unlikely that the brain explicitly encodes all dynamic situations. Specifically, the hypothesis of time compaction provides a solution that the brain could exploit to drastically reduce the amount of information introduced by the time dimension, rendering fast responses in complex scenarios an achievable feat.

Time compaction has been proposed as a decision-making framework, aimed to describe how cognitive agents may be able to cope with dynamic environments in real time. In this definition, cognitive agents refer to decision-making capable agents, and dynamic environments are interpreted as scenarios with moving, displacing elements that may or may not interact in some point of their trajectories (i.e. collide or cross in a proximal future). According to time compaction most defining assumption, the challenge of spatiotemporal cognition can be

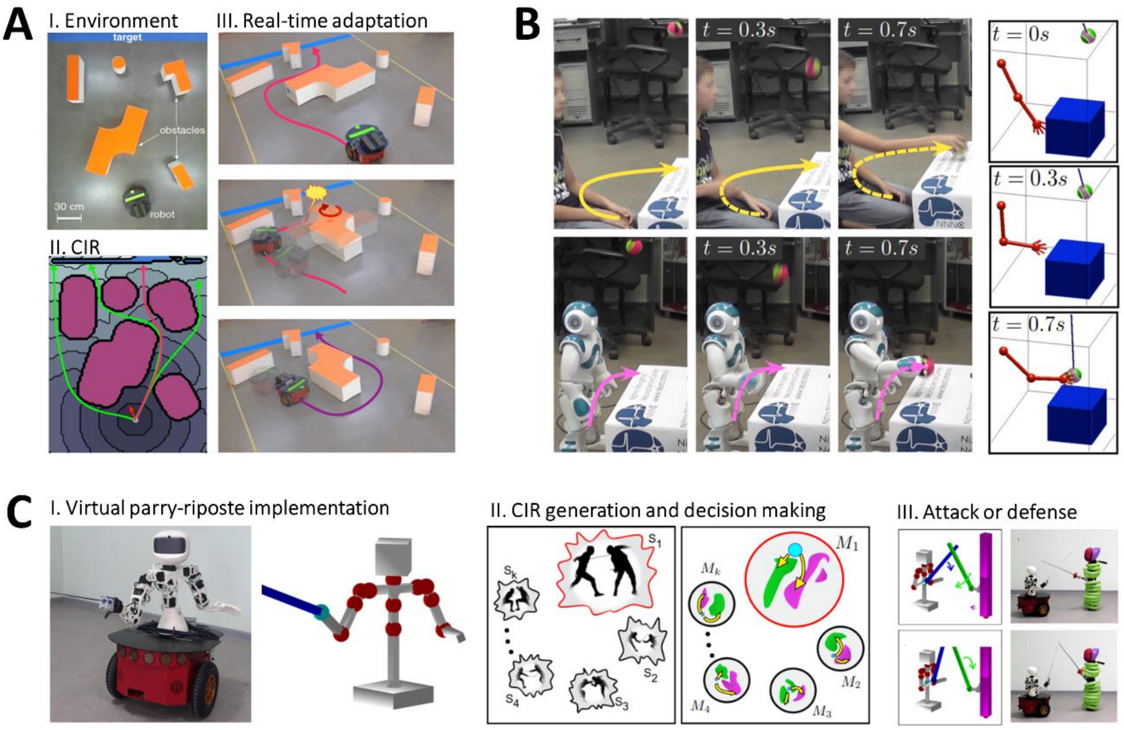

Figure 7. Applications of time compaction. A Simple automatas can exploit time compaction to safely navigate around obstacles. After comprehending the environment, a CIR that contains future collisions as well as potential routes of navigation is generated. The automata can also adapt its course of action after unexpected changes in the environment (e.g. twisting of the central block). Adapted from Villacorta-Atienza & Makarov (2016). **B** A robot equipped with CIRs mimicks human cognitive ability. The cardboard box is mapped as a static obstacle, depicted as a blue cube in the simulation of the robot arm movement (right panels). The robot arm follows the trajectory provided by the simulation and catches the falling ball. Adapted from Villacorta-Atienza et al. (2017). **C** Robotic fencer equipped with CIRs engages in a parry-riposte task. Joints in arms and torso are simulated in a virtual environment, where CIRs comprising multiple strategies are constructed. Finally, results are validated in real attack or defense situations. Adapted from Calvo et al., (2020).

addressed by integrating the known functional bases of spatial cognition with specific mechanisms dealing with time (Villacorta-Atienza et al., 2010). As such, a cognitive agent immersed in a dynamic environment will compact all the time-dependent features of its surroundings into a single, static internal representation of future interactions and optimal decision strategies. Solely the spatial coordinates of events predicted to be relevant are preserved, stripping any temporal dimension off the situation. This construct is called a Compact Internal Representation (CIR), where an internal representation can be envisioned as a mental map of spatial predictions. The collapse or compaction of the temporal dimension remarkably reduces how much information is to be operated by the brain, which enables efficient processing and learning of time-changing situations and construction of sophisticated behaviours in real-time (Fig. 7) (Calvo et al., 2020; Villacorta-Atienza et al., 2017). Therefore, time compaction proposes a paradoxical formula: to deal with time effectively, the brain eliminates time.

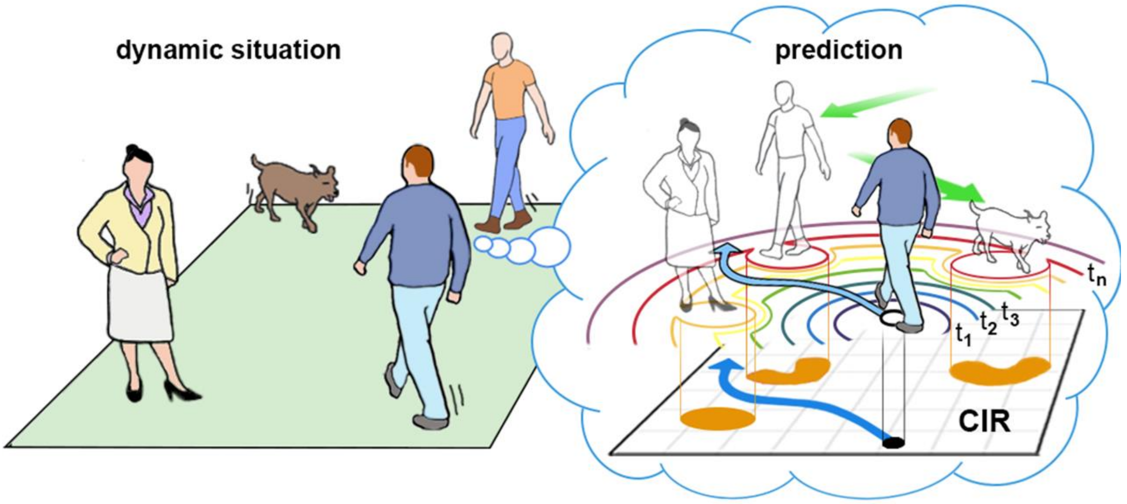

Figure 8. Hypothesis of time compaction. To safely navigate in a dynamic situation (left), the subject (blue clothes) generates a CIR of the environment (right bubble). The CIR is predictions of the expected behaviour of other parties (green arrows), alongside simulations of the own subject's positions at different times t_1, t_2, …, t_n (coloured curves). Potential collisions (interactions) correspond to coincidences between the subject and other parties' future positions, and are represented in the CIR as virtual static obstacles (yellow areas). The CIR includes the optimal trajectory that avoids predicted obstacles (dark blue arrow), allowing safe navigation in the real world (light blue arrow). Adapted from Villacorta-Atienza et al. (2021).

The hypothesis can be easily illustrated through an example of a subject walking in a crowd (Fig. 8). Here the navigation is considered from an egocentric perspective, thus considering that the cognitive agent (pedestrian) is immersed in the situation and is susceptible of taking actions. According to time compaction, the subject processes the situation by predicting the evolution of its surroundings and simulating any possible movements at successive time instants, denoted as possible future positions. This way, the coincidences between the virtual locations of the subject and other parties correspond to future collisions. These predictions are mental static obstacles, since the pedestrian cannot traverse them in the future. Their spatial arrangement, according to the subject's reference framework, is what constitutes the CIR. For safe navigation, the subject can now simply avoid virtual static obstacles as if they were real. Because a CIR is thought to act as a decision space, the route or action planning most beneficial to the cognitive agent should also be mapped onto it, constructing an internal representation of the outside world that has: i) dynamic elements reduced to static interactions and ii) effective courses of action. To account for the nature of these kind of interceptive actions, time compaction uses time-to-collision curves, as suggested by timing performance experiments (Novak, 1997; Tresilian, 1995). Nonetheless, time compaction enhances the contribution that spatial dimension makes to the processes supporting the temporal features of interactive tasks. The paradigm shift discussed in this work is grounded on the notion that brain abandons the time dimension and works exclusively on the space domain to address critical challenges in the biology of complex behaviour.

The CIR potential goes beyond its role as a substrate for actions. CIR provides a natural framework for learning and building memories of dynamic situations. This paradigm allows storing previous experiences in a “library”. Then, such a CIR library can be used for fast navigation and manipulation by recalling the CIRs corresponding to given situations. Based on these features, it is hypothesized that time compaction is a cognitive mechanism mainly involved in survival-like decision making, e.g., attack or defensive strategies during agonistic behaviours (fighting), trajectories generation (chasing and escaping), and coordination of actions among several agents (hunting).

Because of this dual-layered nature of the CIR (interaction-decision), the condition that cognitive agents must be able to make choices is necessary but not sufficient. There must also be a motivational will, for the agent to set a preferred goal and course of action aimed to successfully resolve a given dynamic situation. This makes time compaction applicable to both robotic automatas with scripted motivations (Calvo et al., 2016) and, theoretically, to animals with advanced, not stereotyped volition. Even though time compaction arises in artificial neural networks with simple architectures (Villacorta-Atienza et al., 2013), to this moment only highly-encephalized animals should be considered as potential candidates for possessing cognitive strategies salient enough to be experimentally assessed. Alongside accessibility matters, that makes mammals and particularly humans the premiere testbed for time compaction, although vertebrates in general (i.e. birds, sharks) and certain invertebrates (i.e. octopuses) might also be tentative contenders.

In summary, time compaction provides action-based internal representation of static situations that can generalize to dynamic scenarios, known as CIRs. These CIRs would be fundamental building blocks of cognition mediating flexible interaction with time-changing environments. CIRs contain simultaneous simulations of all possible outcomes of an organism’ actions, which can be attained by representing the temporal evolution of a situation as predictive maps of future spatial interactions. However, to this day there’s been a lack of testing the biological soundness of this hypothesis. The present work shows experimental evidence that time compaction is an actual mechanism in the human brain (Villacorta-Atienza et al., 2021), and goes on to provide mathematical modelling of the phenomena both at behavioural and neuronal levels.

2. OBJECTIVES

The main hypothesis that structures this thesis dissertation is that time compaction is a cognitive mechanism present in the human brain. Until now, time compaction has been restricted to the theoretical plane and its application to robots. By providing empirical evidence showing that dynamic situations share the same processing principles that govern the comprehension of static scenarios, this work paves the way to a unified paradigm of cognition based on the capacity of the brain to generalize from experience. A direct consequence is that time compaction can be easily implemented on top of the knowledge about the internal representation of time-invariant phenomena that is already available and widely accepted by the scientific community. Moreover, by demonstrating that complex cognitive functions operate under the same framework that has already been proven functional in robots, this work could open a venue to new insights into more naturalistic human-robot interactions.

Thus, the overall aims and the particular objectives of the present thesis are as follows:

AIM 1. To assess the biological soundness of time compaction.

- *Objective 1.1.* Test the saliency of time compaction in dynamic scenarios.
- *Objective 1.2.* Evaluate human performance in a discrimination learning task.
- *Objective 1.3*. Determine the age onset of time compaction in humans.

AIM 2. To develop a behavioural model of time compaction.

- *Objective 2.1.* Formulate a model based on learning and memory.
- *Objective 2.*2. Parametrize the model to simulate human performance.
- *Objective 2.3.* Measure the fit of the model to experimental data.

AIM 3. To develop a neuronal model of time compaction.

- *Objective 3.1.* Design a biological neural network capable of learning and retrieval.
- *Objective 3.2*. Evaluate the emergence of pattern completion compatible with time compaction.
- *Objective 3.3.* Measure the advantage of time compaction under neural competition.

3. METHODOLOGY

3.1. Behavioural paradigm to test time compaction

To reveal the existence of time compaction, a behavioural methodology based on stimulus generalization is proposed (Guirlanda & Enquist, 2003; Pfeuffer et al., 2018). It's been inspired by classic experiments that study the cognitive processes involved in collision perception tasks (Law et al., 1993; Tresilian, 1995) and by the Stroop interference effect in working memory (Kiyonaga & Egner, 2014; Stroop, 1935)

Experimental validation of time compaction requires testing compacted versus non-compacted situations. In a natural context, time compaction is essentially idiothetic, in the sense that a subject takes active part in a situation and affects the situation directly. Therefore, potential interactions that may lead to time compaction are always present. Such ubiquitous phenomenon provides an exploitable bias suitable for experimental testing.

Nonetheless, the working hypothesis states that for time compaction to be a salient cognitive mechanism, it should not depend on whether or not the subject participates in a situation. For that reason, the experiments were designed from an allocentric point of view. The subject's purpose is then to observe without influencing the situations. The participants were provided with two types of visual stimuli:

1. Circles moving on a computer screen approaching in collision trajectories (Fig. 9A). Note that collision is not displayed on the screen, but the brain virtually constructs it. In this case, as there is a predicted interaction between the circles (collision), time compaction plays a role and the situation is compacted and represented in the brain exclusively by the colliding area (CIR in Fig. 9A).
2. The same moving circles, but in crossing instead of colliding trajectories (Fig. 9B). As there is no future interaction expected between the circles, the subject is not able to compact the situation and resorts to represent it as a spatiotemporal structure (using initial positions, speeds, trajectories, etc.). Note that, following time compaction, option 1 is less demanding than option 2 for the brain.

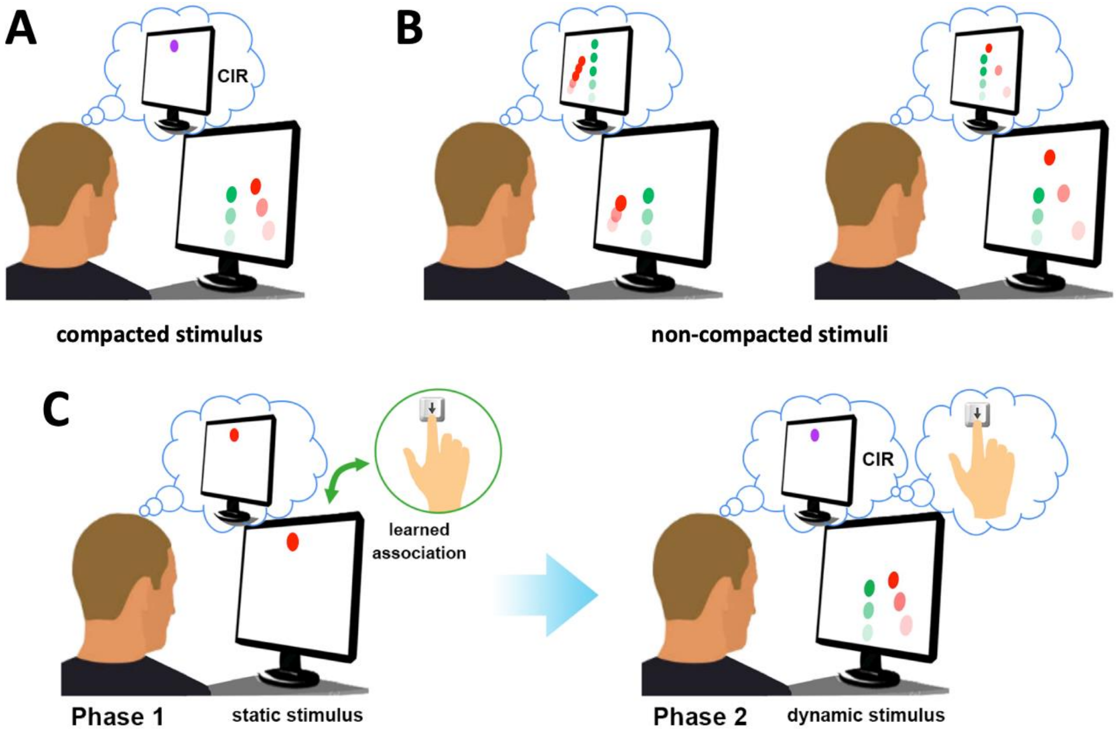

Figure 9. Rationale for the experimental assessment of time compaction in allocentric context. A Dynamic stimulus with predicted future interactions are internally compacted and represented by its collision area (no temporal dimension). **B** Dynamic stimuli with no predicted collisions are not compacted and are instead represented as events with temporal dimension. **C** Concatenation of two experimental phases. According to time compaction, a dynamic stimulus whose CIR matches a static stimulus will be closely related in memory. First, a subject learns a specific association between the static stimulus and the arrow key (e.g., the down-arrow key) in phase 1 (left). Then, in phase 2 (right), the displayed dynamic stimulus will be represented by its CIR, whose resemblance with the static stimulus will recall the same stimulus-key association, and thus the subject will press the same arrow key with more likelihood. Note that circles' speed is illustrated by circles' separation, so closer or further consecutive circles denote slower or faster movement. Adapted from Villacorta-Atienza et al. (2021).

Experimentally verifiable predictions of time compaction

The core idea is the similarity between the internal representations of dynamic and static situations, which can be exploited by tailoring a two-phase experiment based on stimulus generalization (Fig. 9C). In the first phase, participants were shown single, static circles on the screen. During the second phase, they are exposed to dynamic circles, either in motion towards collision (interaction) or crossing (non-interaction) trajectories. The stimulus generalization takes place when a behavioural response is associated with a specific stimulus, and afterwards a novel stimulus sharing the same features triggers the same answer.

The only action participants are required to perform is to associate what is displayed in the screen with the keyboard's up and down arrow keys, by means of a trial-and-error discrimination test. Because it is an allocentric situation, planned actions (pressing up or down key) shouldn’t share a common representational space with predicted interactions (collisions), as opposed to the egocentric situations. Therefore, the only means of linking an action with its action-stripped CIR under these circumstances should be resorting to associative working memory, whose access can be modulated by interference (Kiyonaga & Egner, 2014). The relationship that static and dynamic stimuli should have at the representational level is exploited here to cause that interference. A dynamic stimuli consisting in two circles whose trajectories would collide at coordinates *XY* of the screen should have a CIR consisting in a single circle, positioned precisely at those collision coordinates *XY*. Likewise, a static stimuli consisting in a single circle positioned at coordinates *XY* of the screen should have a CIR consisting in that same circle positioned at coordinates *XY*. Therefore, both stimuli would share the same CIR, that is a single circle at *XY*. Due to the allocentric nature of the task, both representations would be action-stripped CIRs, with the corresponding up or down arrow key linked to them by associative memory. What would happen then if participants first learn to associate the static stimuli to a given arrow, and then they are asked to find that association again for the dynamic stimuli? If both stimuli share the same CIR and arrow key, then learning the static first should facilitate learning the dynamic one, because internally they are effectively the same. On the contrary, if the arrow key associated to them was opposite, learning the static first should hamper the learning of the dynamic one, because the established arrow-CIR association would need to be undone and replaced by a different one.

Therefore, if the hypothesis that static and dynamic situations are represented internally in a similar way is correct, then prior learning of specific static scenes should speed up or slow down the posterior learning of dynamic situations. The sign of the effect will be determined by the similitudes and differences of the CIRs of dynamic and static conditions.

Overview of experiments

Different configurations of dynamic and static stimuli were designed to test time compaction predictions and to eliminate other explanations of this phenomenon. The participants were prompted to discover two hidden rules relating the stimuli with the up- and down-arrow keys, by trial-and-error (Fig. 10A). The assignment of the keys was random for each participant. All participants were randomly assigned into four groups: (1) Control, (2) Favored, (3) Hampered, and (4) Validation.

The first three groups of participants comprise the time compaction’s experimental assessment *per se*. During phase 1 (Fig. 10A, top panel), each subject observes static stimuli in a trial-by-trial basis (1.5 s/trial), one at a time and randomly chosen from a set of three static situations pertaining to its group (Fig. 10B, top panel). Upon the stimulus' disappearance, the participant would press one of the arrow keys, either up or down. If there is a match between the pressed and the key associated to hidden rule 1, the participant receives a green tick that symbolizes positive feedback; otherwise, a red cross is displayed. The process is repeated until the participant figures out hidden rule 1, associating the correct keys with the static situations.

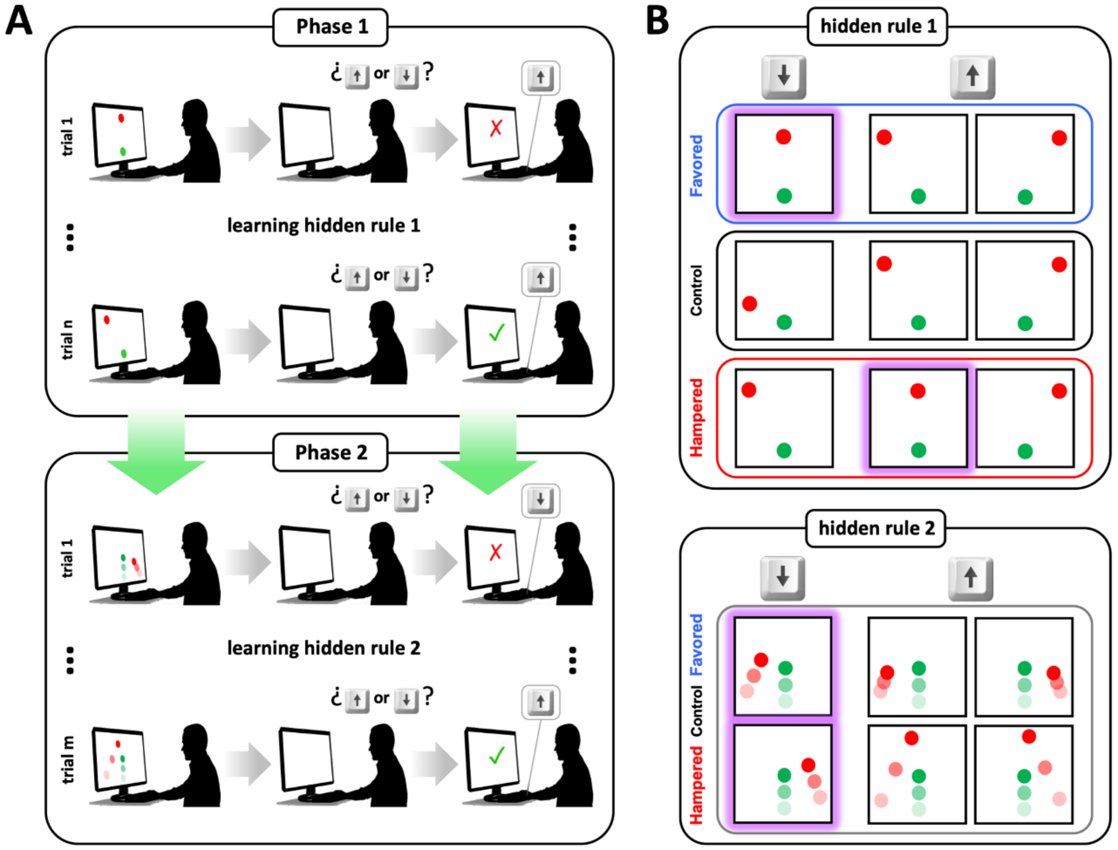

Figure 10. Experimental procedure. A Phases 1 and 2 are performed consecutively. In each phase, participants are prompted to find a hidden rule associating the up and down arrow keys with stimuli shown on the screen. After every trial positive or negative feedback is provided, depending on whether or not the pressed key agreed with the true hidden rule. **B** All stimuli are comprised of red and green circles. The three static stimuli of phase 1 are associated to the arrow keys by hidden rule 1. The green circle is located at the middle bottom part of the screen in all static stimuli, whereas the red circle is at the upper part of the screen for the Favoured and Hampered groups, and laterally above the green one for the Control group. Arrow key assignment is randomly established at the beginning of the experiment for each participant, and differs among Favoured, Control, and Hampered groups. Note that the green circle is intended as a spatial reference to distinguish centre from sides and does not carry information necessary to find the hidden rule. In phase 2, arrow keys associate with six dynamic stimuli, two dynamic matching (DM), and four non-dynamic matching (non-DM) stimuli (all dynamic stimuli depict the green circle moving upwards vertically, and the red one upwards diagonally). Hidden rule 2 is the same for all these groups. The static and dynamic matching stimuli (SM and DM) are highlighted in purple. The picture shows one of the two possible assignments of arrow keys as an example; in the other case, arrows are exchanged.

Once phase 1 has been completed (i.e., hidden rule 1 discovered), the participant enters phase 2 (Fig. 10A, bottom panel). Now the displayed stimuli are randomly extracted from a pool of six dynamic situations (Fig. 10B, bottom panel), and again, the participants should discover the hidden rule 2 associating stimuli with up- and down-arrow keys.

Additional participants were recruited to a separate validation group, so any potential biases inherent to phase 2 that might be affecting the learning process could be discarded. These subjects skip phase 1 and tackle phase 2 directly. Their learning performance was measured as in the above mentioned time compaction experiments. Hence, any internal discrepancy between phase 2 in the validation group and time compaction in the experimental groups would be attributed to prior exposure to phase 1.

Stimulus combinations for different groups of participants: Expected learning performance

Specific static and dynamic stimuli were designed to test the predicted modulation of the learning performance. Static situations are made up of a green and red circle, each positioned at different computer screen locations (Fig. 10B, top panel). There are three sets of static stimuli specific to each experimental group. In phase 2, all groups receive the same set of dynamic stimuli consisting of six videos displaying two moving circles: one always in motion upwards on the same vertical trajectory, and the other one moves upwards and in diagonal (Fig. 10B, bottom panel). It is important to stress that collisions were never displayed, as the circles disappear before crossing or colliding. These dynamic scenes presented during phase 2 are comparable to the stimuli employed to study the cognitive mechanisms used by humans in collision situations.

The hypothesis of time compaction is grounded on the functional similitude of the internal representations of dynamic and static situations. From this perspective, one static and two dynamic stimuli ought to be identically represented in the brain (Fig. 10C and Fig. 10B, highlighted in purple). These are referred to as static matching (SM) and dynamic matching (DM) stimuli. The experimental groups differ by the use of SM and hidden rules:

- Control group: No SM among the static stimuli (Fig. 10B, top panel, Control). Therefore, the CIRs for static and dynamic stimuli are different, and hence no connection between hidden rules 1 and 2 exists. Thus, learning in phase 2 is independent of phase 1. The results of this group are used as control for monitoring the performance of other groups of participants.
- Favoured group: In this case, the SM (Fig. 10B, top panel, Favoured; highlighted in purple) and two symmetric DM (Fig. 10B, bottom panel; highlighted in purple) are

displayed in phases 1 and 2, respectively. For a given participant, both the SM and DMs might be associated by chance with the down-arrow key. Then, according to time compaction, a match exists between hidden rules 1 and 2. After learning the hidden rule 1, the subject creates the association: ‘‘SM-down key”. Then, time compaction predicts that when the DM appears during phase 2, the subject will recall its CIR, which is similar to the SM, and hence there is an increased likelihood that the down key will be pressed, which is the correct choice. Thus, subjects in this group will learn faster during phase 2, compared to the other groups.

- Hampered group: This group is similar to the Favoured group, but now in hidden rule 1, the SM and one non-SM are interchanged (Fig. 10B, top panel, Hampered). Thus, hidden rules 1 and 2 relate the SM and DM to opposite keys and, following the example, SM and up key will be linked. In this case, after learning hidden rule 1, the participant will be surprised at the presentation of the DM, since the ‘‘logical” response ‘‘up key” will produce an error. Then, an effort to ‘‘forget” or “re-learn” the previous association and establish a new one will be required. As a result, subjects in this group will learn at a slower pace during phase 2.

Conceptual constraints

The experimental procedure above described was carried out to disclose time compaction as a salient cognitive mechanism for dealing with dynamic situations. To emphasize, the CIR acts as a cognitive substrate for planning and decision-making. That is to say time compaction is a primary mechanism that occurs independently on such high-level processes. Thus, prior training of the participants was unnecessary. Nonetheless, before performing the experiment, it was reassured that participants were not aware of (1) the nature of the experiment, (2) a possible relationship between static and dynamic stimuli, and (3) how essential collisions are; so they were entirely clueless regarding the scope of the task.

Experimental design

410 university students and graduates (adults) were engaged in the study. None of them reported prior attentional problems. All subjects had normal or corrected-to-normal vision, were naïve to the study purpose, and had no experience with the tasks and stimuli used here. Mean age of the participants was 21.08 years for women and 22.46 for men (95% confidence intervals [19.98, 22.17] and [21.08, 23.84]; no significant difference, Welch test $p = 0.12$).

Experiments were conducted over randomly composed groups of men and women. The final sample of n = 261 subjects (135 women and 126 men) for Control (35 women, 40 men), Favoured (52 women, 48 men) and Hampered (48 women, 38 men) groups comprised participants who fulfilled the task showing a stable performance (see Technical Appendix), i.e., with the learning lengths not exceeding 46 trials (82% out of a sample of 318). Most subjects completed the experiment within 10 min. The other 92 participants (50 women and 42 men) were assigned to the Validation group. All subjects provided informed consent for their anonymous participation in accordance with the experimental procedures, approved by the Institutional Review Board (Committee of Bioethics, National Distance Education University). All experiments were performed following the guidelines and regulations set forth by the Declaration of Helsinki.

Procedure

Participants were subjected to a computer-based trial and error training. The experiment in the Control, Favoured, and Hampered groups consisted of two phases: static conditioning (phase 1) followed by dynamic testing (phase 2) (Fig. 3A). The Validation group was tested in phase 2 only (i.e., skipping the phase 1). All subjects completed the procedure individually, as no interaction between them was allowed.

The experimental protocol was implemented on table-top computers by using MATLAB v17 (MathWorks). Static and dynamic situations were shown on the computer screen for 1.5 s and contained either two static or two moving circles of a diameter of 1 cm coloured in red and green and presented on a white background (Fig. 3B). Circles were chosen to avoid prior cognitive bias (Reed & Vinson, 1996). In the static situations, a green circle was added as a geometric reference to facilitate the distinction between stimuli with the lateral and central red circles. This also smoothed the passage from the static to the dynamic phase (all the time showing two circles). During phase 2, the green circle always moved upwards vertically with a velocity of 4.5 cm/s. The red circle moved upwards diagonally with one of the three velocities: 1/3, 2/3, and 4/3 of the speed of the green circle. The initial position of the red circle was chosen in such a way that the velocity ratio 2/3 corresponds to circle collision, i.e., to the DM stimuli. In the DMs, collision is not shown on the screen but would take place 1 s after the circles disappear (recall that circles were displayed during 1.5 s).

Before each experiment, a researcher read aloud a brief instruction to be followed by the participants, which was also shown on the screen. Any question asked by the participants was answered by citing the instructions again. There was no mention to the connection between phases. The structure of the instruction was as follows. First, it says that the experiment consists of a static stage, followed by a dynamic stage. The objective is to find out the relationship between the displayed situations and the up/down arrow keys. In the static stage, the instruction specified that the green circle is located at the bottom centre of the image, whereas the red circle appears randomly at the upper left, right or centre of the screen (Favoured/Hampered groups, in Control the upper centre is replaced by a non-matching bottom circle). In the dynamic stage, both green and red circles move along straight lines at a constant velocity. While the green circle always starts from the bottom centre and moves upwards vertically at the same velocity, the red circle changes its velocity from trial to trial randomly (to reproduce collision and crossing situations), and can appear at the bottom left or the bottom right of the screen.

There was no time limit to complete both phases 1 and 2. However, there was a maximum of 80 trials per phase. This hard limit was based on pilot studies where participants were allowed 100 trials. A subject was considered to have learned the hidden rule if at least 18 correct responses were achieved in the last 20 trials. In this case, the experiment stopped, and the trial at which the participant reached the criterion was considered the learning length. Note that a 20 trial range corresponds to the expectation of the number of trials such that every situation appears at least twice.

After completing phases 1 and 2, participants were prompted to write down the underlying association rule, which in their opinion, best explains the relationships between the displayed situations and the arrow keys. At the end of the experiment, the participants filled out a form containing information about age and gender.

Statistical analysis of data

The sequence of responses of each participant was recorded during the experiment, so performance could be assessed later on. Learning performance was assessed in phase 2 both at the population level, as the average number of successful answers per trial (success rate), and at the individual level, as the number of trials required by each participant to learn the rules (learning length) (Fig. 11). The same metrics were also used to quantify the learning performance of subjects in the Validation group.

Estimation of time-to-event curves: A time-to-event function represents the probability that a certain proportion of individuals had learned hidden rule 2 at a given trial. It was obtained through the Kaplan-Meier nonparametric estimator (Peterson, 1977). To assess whether gender

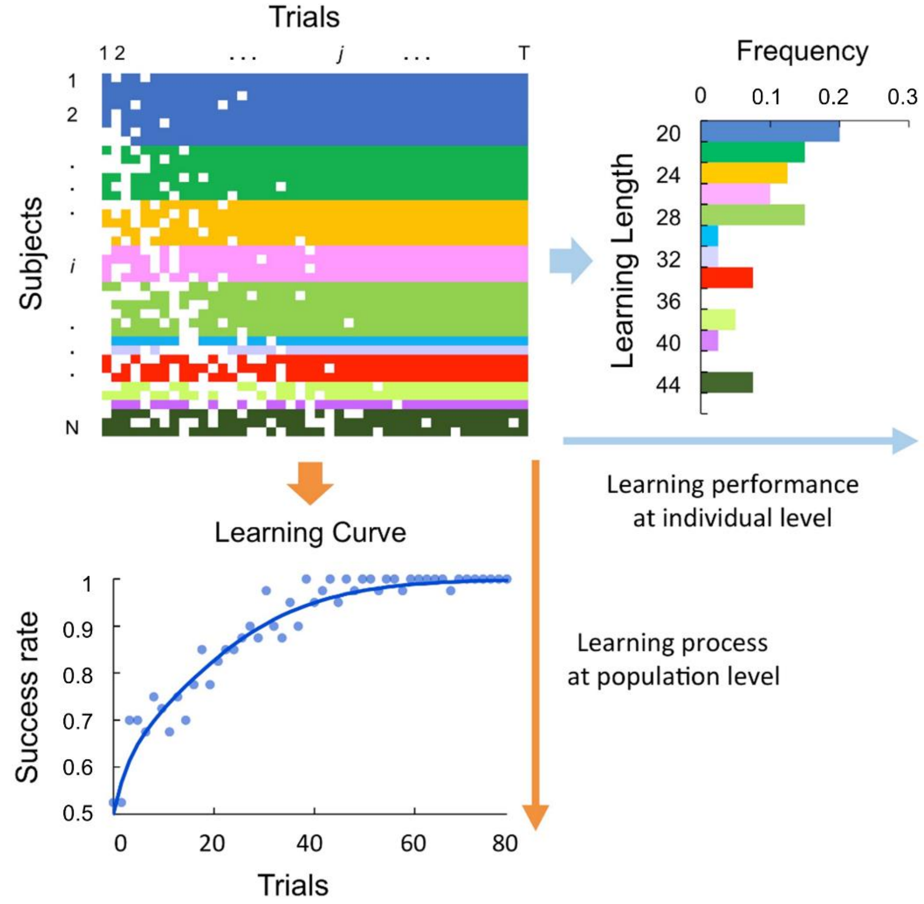

Figure 11. Data structure and analysis of data. The experimental results are structured in a binary matrix of fails (white squares) and successes (colored squares), per subject and trial. In the above representation participants with the same learning length are grouped by color. Collapsing the rows dimension give a mean success rate per trial, enabling the analysis of the learning process at population level. Collapsing the columns dimension using predefined criteria (learning defined as 18 successes out of 20 trials) allows analyzing learning performance at individual level via the frequency distribution of learning lengths.

and experiment might simultaneously affect the time-to-event curves estimation, a multivariate Cox proportional-hazards regression model was fitted (Jahn-Eimermacher et al., 2011). The model assumptions were checked via the Schoenfeld test (Abeysekera & Sooriyarachchi, 2009; Schoenfeld, 1983) and residuals plots against time for each covariate. The Cox model was extended to allow for time-dependent coefficients (Saegusa et al., 2014) using a step function, dividing the sample into three learning length intervals: < 20, 20–46, and > 46.

Estimation of learning curves: General estimating equations (GEE) were used to model the probability of success at a given trial since it allows taking into account different correlation structures in the data (Hanley et al., 2003; Hardin, 2005; Hin and Wang, 2009). Binomial ‘‘logit” was used as a link function given the dichotomous nature of the response variable (either fail a trial or not). A backward stepwise elimination procedure was followed to select the minimal set of variables with a significant explanatory power. Variables taken into account were gender, group, trial number, and their interactions. Successive nested models were compared using the F-test and the Quasilikelihood Information Criterion (QIC) (Pan, 2001). The interaction terms were interpreted separately for gender and experiment. To ensure that the model characterized the learning phase, only the set of trials with a mean success rate lower or equal to 0.99 were considered. A factor representing the different researchers that conducted experiments was introduced in the model, and no significant effect was found (F-test, p = 0.21). Thus, there was no detectable bias introduced in the results by the researcher, which confirms the reproducibility of the experimental approach.

Association rule verbalization and response time: Potential relationships between the verbalization of the association rules found by the participants and the learning length were explored by using a Generalized Linear Model (GLM) with a binomial ‘‘logit” link function. Regarding verbalization, 96.2% of participants (251 from 261) expressed the dynamic rules in two main categories: in ‘collision’ terms (containing words as collision, crash, finding, etc.) or in ‘velocity’ terms (with words as velocity, speed, etc.). The remaining participants (10 from 261 or 3.8%) wrote the dynamic rule by mixing ‘collision’ and ‘velocity’ terms or using spatially related descriptions based on directions, positions, etc. The learning lengths were divided into four groups: less or equal to 20 trials, 21-30, 31-40, and 40-46. The differences in response time due to experiment or gender were checked by fitting a GEE with a gaussian ‘‘identity” link function and considering the response time as a continuous response variable.

Table S1 (Technical Appendix) provides a comprehensive description of all statistical comparisons (sample size, test, sample statistic value, p-value). All statistical calculations were performed in R v3.3.1, using the packages *surviva*l (Therneau, 2015), *survminer* (Kassambara et al., 2017), *geepack* (Halekoh et al., 2006), *stat* and *base* (R Core Team, 2013), and *dplyr* (Wickham et al., 2017).

Task complexity

In order to monitor the influence of intrinsic difficulty of stimuli over experiment performance we defined an index quantifying the difficulty to figure out phase 2 association rule when a specific sequence of stimuli is displayed.

Let consider a sequence *s* of length *l* made up of *m* stimuli randomly distributed. Six possible stimuli ($m \leq 6$) are considered, corresponding to phase 2. Let d_{ij} denote the distance between the *j*-th repetition of the stimulus *i* ($i = 1, \dots, m$) and its previous appearance, and by r_i the number of repetitions of the stimulus *i* in the sequence *s* ($\sum_{i=1}^{m}(r_i + 1) = l$). The difficulty of the stimulus *s* is quantified by evaluating the probability of learning the association rule when it is displayed in Control conditions. Assuming an exponential-decay recall process, the probability of recalling the correct association key for the specific stimulus *i* of the sequence *s* (and learnt after the first appearance of *i* in *s*) will be

$$e^{-ad_{ij}} \qquad (1)$$

where *a* is the decay constant. This way, the probability of answering correctly from the stimulus *s* will be given by

$$p(s,a) = \prod_{k=1}^{l} p(k,s,a) \qquad (2)$$

where $p(k,s,a)$ stands for the probability of correct answer (right association key) at trial *k*, where the stimulus *i* ($i = 1, \dots, m$) is presented. Therefore, making explicit the probability for each one of the *m* different stimuli in *s*, $p(s,a)$ can be written as:

$$p(s,a) = \left(\frac{1}{2}\right)^{m} \prod_{i=1}^{m} \prod_{j=1}^{r_i} e^{-ad_{ij}} = \left(\frac{1}{2}\right)^{m} \prod_{i=1}^{m} e^{-a\sum_{j=1}^{r_i} d_{ij}} = \left(\frac{1}{2}\right)^{m} e^{-a\sum_{i=1}^{m}\sum_{j=1}^{r_i} d_{ij}} \qquad (3)$$

Applying logarithm to both sides of this expression,

$$\log\big(p(s,a)\big) = \log\left(\left(\frac{1}{2}\right)^{m} e^{-a\sum_{i=1}^{m}\sum_{j=1}^{r_i} d_{ij}}\right) = -m\log 2 - a\sum_{i=1}^{m}\sum_{j=1}^{r_i} d_{ij} \qquad (4)$$

Note that the decay constant *a* is a scale factor for the distance *d*, common to all stimuli. Therefore, without loss of generality, *a* = 1 can be considered. On the other hand *m* = 6 for all stimuli, so the factor *m* log(2) will be a common onset. Therefore, from Eq. (s3) we define the *difficulty of stimulus s*, denoted by *D*(s) as:

$$D(s) = \sum_{i=1}^{m}\sum_{j=1}^{r_i} d_{ij} \qquad (5)$$

The stimulus difficulty defined in Eq. (5) strongly depends on the stimulus length *l*. Thus in order to define a difficulty index that can be compared among stimuli of different lengths: 1) it was generated a set of samples where each sample was made up of 100.000 randomly-generated stimulus sequence of equal-length *l*, where each one consists in a stimulus sequence of length *l* with six different stimuli randomly distributed; lengths *l* vary between 20 and 80 so 61 samples were generated. 2) For each sample, it was obtained the normalized frequency distribution of the difficulty, $f_l(c)$, where *l* denotes the length of stimuli in the sample and c is the class containing the difficulty. 3) Finally, given a stimulus s of length *l* and difficulty *D*(*s*), it was quantized its *stimulus difficulty index DI*(*s*) by its cumulative frequency in $f_l(c)$, i.e:

$$DI(s) = \sum_{c=1}^{c_D} f_l(c) \qquad (6)$$

where c_D denotes the class containing the difficulty *D*(*s*) of the stimulus *s*.

Experiments on children

A sample of 386 children was collected from three different elementary school institutions. All subjects had normal or corrected-to-normal vision, were naïve to the study purpose, and had no experience with the tasks and stimuli used here. Mean age of the participants was 10.05 years for girls and 10.01 for boys (95% confidence intervals [9.92, 10.19] and [9.86, 10.15]; no significant difference, Welch test p = 0.63).

Experiments were conducted over randomly composed groups of boys and girls. Most subjects completed the experiment within 15 minutes. Parents of all participants provided informed consent for their anonymous participation in accordance with the experimental procedures, following the guidelines and regulations set forth by the Declaration of Helsinki.

Participants were subjected to the same computer-based trial and error training task performed on adults. All the procedures described for adult participants apply here, except for: (1) Experimental groups comprised solely Favoured and Control conditions, (2) in phase 2 non-DMs corresponding to red circle's velocities of 1/3 and 2/3 were removed from the setup, (3) maximum number of trials allowed was 60, to avoid frustration that could affect learning performance. Statistical analysis of learning performance followed the same guidelines as stated above for experiments on adults

3.2. Probabilistic model of time compaction

Mathematical rationale

Consider the random variable S that denotes the success in the participant's answer when a dynamic situation is displayed. Therefore, $S = 1$ / $S = 0$ stands for correct/wrong answer respectively, i.e. the pressed key matches / does not match with the displayed dynamic situation according to the underlying testing association rule.

Consider also that a recall process exists, described by a random variable *R*, with *R* = 1 or 0 if the subject recalls or not the corresponding stimulus. Assuming the recall process is present during the experiments, the probability of getting a correct answer when the stimulus *i* appeared *t* time units ago will be

$$P(i\ appeared\ t\ time\ ago) \equiv P_{i,t}(S=1) = P_{i,t}(S=1 \cap R) =$$
$$= P(R=1)P_{i,t}(R=1) + \ P(R=0)P_{i,t}(R=0) \qquad (7)$$

The recall probability will be

$$P_{i,t}(R=1) = e^{-at} \qquad (8)$$

where *a* is the recalling decay rate, whereas the probability of non-recalling will be

$$P_{i,t}(R=0) = 1 - P_{i,t}(R=1) = 1 - e^{-at} \qquad (9)$$

The model assumes that when the subject undergoes recalling, the answer will be always correct, so

$$P(R=1) = 1 \qquad (10)$$

and when the subject does not recall, the answer will be random. Thus

$$P(R=0) = \frac{1}{2} \qquad (11)$$

This way, from Eq. (7), the probability of getting the right answer by recalling the key associated with the stimulus *i* (learnt *t* time ago) will be

$$P_{i,t}(S=1) = e^{-at} + \frac{1}{2}(1 - e^{-at}) = \frac{1}{2} + \left(1 - \frac{1}{2}\right)\ e^{-at} = \frac{1 + \ e^{-at}}{2} \ (12)$$

Assuming now that 1) time is discrete, measured in terms of *trials* and 2) the stimulus *i* has appeared at the trial *T*. Thus the probability of right answer will depend on when the stimulus *i* previously appeared, since the association rule will be learnt once it appears, but the recalling will depend on the distance (in trials) between its previous and present appearances.

Analytical model

As the involved recalling process is only considered when a single stimulus appears up to three times, if this stimulus appears four or more times it is assumed the corresponding association will be always recalled and the probability of successful answer will be 1.

In order to systematize the model, the random variable X_i is defined as the number of times the stimulus *i* appeared in the interval [1, …, *T*-1]. Thus the overall probability of success when stimulus *i* has appeared at the trial *T* can be written as:

$$P_i(S=1) = P_i(S=1 \cap X_i=0) + P_i(S=1 \cap X_i=1) + P_i(S=1 \cap X_i=2) + P_i(S=1 \cap X_i \geq 3) \qquad (13)$$

where subindex *i* denotes probabilities referred to the stimulus *i*.

Analysing separately the four terms in the right side of Eq. (13), if the stimulus hasn't appeared yet in [1, …, *T*-1] (so it appears for the first time at trial *T*), there's no prior information, so the subject will press one of the two keys randomly, i.e. $P(S=1\,|X_i=0)=1/2$, and

$$P_i(S=1 \cap X_i=0) = P_i(S=1\,|X_i=0)\cdot P_i(X_i=0) = \frac{1}{2}\left(\frac{5}{6}\right)^{T-1} \quad (14)$$

If the stimulus has appeared once previously, then

$$P_i(S=1 \cap X_i=1) = \sum_{t=1}^{T-1} P_i(S=1\,|\,X_i=1)\cdot P_i(X_i=1)$$

On the one hand, according to the binomial distribution

$$P_i(X_i=1) = \left(\frac{1}{6}\right)\left(\frac{5}{6}\right)^{T-2}$$

On the other hand, if the stimulus *i* has appeared at the trial *t,* then

$$P_i(S=1\,|\,X_i=1) = P_i(i\ appeared\ T-t\ time\ ago) \equiv P_{i,T-t}(S=1)$$

Therefore,

$$P_i(S=1 \cap X_i=1) = \sum_{t=1}^{T-1} P_{i,T-t}(S=1\,|\,X_i=1)\cdot P_i(X_i=1)$$

$$= \left(\frac{1}{6}\right)\left(\frac{5}{6}\right)^{T-2}\sum_{t=1}^{T-1}\frac{1+\ e^{-a(T-t)}}{2} =$$

$$= \left(\frac{1}{6}\right)\left(\frac{5}{6}\right)^{T-2}\left(\frac{T-1}{2}+\frac{1}{2}\sum_{t=1}^{T-1}e^{-a(T-t)}\right) \quad (15)$$

where

$$\sum_{t=1}^{T-1} e^{-a(T-t)} = \frac{1-e^{-a(T-1)}}{e^{a}-1}$$

Substituting back in Eq. (15)

$$P_i(S=1 \cap X_i=1) = \left(\frac{1}{6}\right)\left(\frac{5}{6}\right)^{T-2} \frac{1}{2}\left[T-1+\left(\frac{1-e^{-a(T-1)}}{e^{a}-1}\right)\right] \quad (16)$$

Considering now that the stimulus *i* appears twice in the interval $t \epsilon [1,\dots,T-1]$, at trials t_1 and t_2, then

$$P_i(S=1 \cap X_i=2) = \sum_{t_1=1}^{T-1}\sum_{t_2=t_1+1}^{T-1} P_i(S=1\,|X_i=2)\cdot P_i(X_i=2)\ (17)$$

The probability $P_i(X_i=2)$ of the stimulus *i* appears twice in the interval $t \epsilon [1,\dots,T-1]$ is given by

$$P_i(X_i=2) = \frac{(T-1)(T-2)}{2}\left(\frac{1}{6}\right)^{2}\left(\frac{5}{6}\right)^{T-3} \quad (18)$$

The probability of recalling the stimulus association depends only on the distance between *T* and t_2, the last trial where the stimulus appeared. Therefore,

$$P_i(S=1\,|\,X_i=2) = P_i(S=1|i \text{ appeared } T-t_2 \text{ time ago}) \equiv P_{i,T-t_2}(S=1)$$

$$P_i(S=1 \cap X_i=2) = \sum_{t_1=1}^{T-1}\sum_{t_2=t_1+1}^{T-1} P_i(S=1\,|X_i=2)\cdot P_i(X_i=2)$$

$$= \left(\frac{1}{6}\right)^{2}\left(\frac{5}{6}\right)^{T-3}\sum_{t_1=1}^{T-1}\sum_{t_2=t_1+1}^{T-1}\left(\frac{1+\ e^{-b(T-\mathrm{t}2)}}{2}\right) \quad (19)$$

Note that the recalling constant is now denoted by *b*. Developing the sum,

$$\sum_{t_1=1}^{T-1}\sum_{t_2=t_1+1}^{T-1}\left(\frac{1+\ e^{-b(T-\mathrm{t}2)}}{2}\right) = \frac{1}{2}\sum_{t_1=1}^{T-1}\sum_{t_2=t_1+1}^{T-1} 1 + \frac{e^{-bT}}{2}\sum_{t_1=1}^{T-1}\sum_{t_2=t_1+1}^{T-1} e^{bt_2} =$$

$$= \frac{(T-1)(T-2)}{4} + \frac{1}{2(e^{b}-1)}\left[(T-1)-\left(\frac{1-e^{-b(T-1)}}{1-e^{-b}}\right)\right] \quad (20)$$

Substituting the Eq. (20) into Eq. (19),

$$P_i(S = 1 \,\cap\, X_s = 2) =$$
$$= \left(\frac{1}{6}\right)^2 \left(\frac{5}{6}\right)^{T-3} \left[\frac{(T-1)(T-2)}{4} \quad + \frac{1}{2(e^b - 1)}\left[(T-1) - \left(\frac{1 - e^{-b(T-1)}}{1 - e^{-b}}\right)\right]\right] \quad (21)$$

The remaining term in Eq. (13) refers to the situation where the stimulus has appeared three or more times

$$P_i(S = 1 \,\cap\, X_i \geq 3) = P_i(S = 1 \mid X_i \geq 3) \cdot P_i(X_i \geq 3) \qquad (22)$$

As the model assumes that the association rule will be always recalled after the stimulus *i* appears three or more times in the interval $t \,\epsilon\, [1, \dots, T-1]$, then $P_i(S = 1 \mid X_i \geq 3) = 1$ so

$$P_i(S = 1 \,\cap\, X_i \geq 3) = P_i(X_i \geq 3) = 1 - P_i(X_i = 0) - P_i(X_i = 1) - P_i(X_i = 2) =$$
$$= 1 - \left(\frac{5}{6}\right)^{T-1} - \left[(T-1)\left(\frac{1}{6}\right)\left(\frac{5}{6}\right)^{T-2}\right] - \left[\frac{(T-1)(T-2)}{2}\left(\frac{1}{6}\right)^2\left(\frac{5}{6}\right)^{T-3}\right] \quad (23)$$

Finally, going back to Eq. (13):

$$P_i(S = 1) = P_i(S = 1 \,\cap\, X_i = 0) + P_i(S = 1 \,\cap\, X_i = 1) + P_i(S = 1 \,\cap\, X_i = 2)$$
$$+ P_i(S = 1 \,\cap\, X_i \geq 3)$$

and substituting the Eqs. (14), (16), (21) and (23) on it, the probability of successful answer when the stimulus *i* appears at trial *T* is described as:

$$P_i(S = 1) = 1 - \frac{1}{2}\left(\frac{5}{6}\right)^{T-1} - \frac{1}{2}\left[(T-1) - \left(\frac{1 - e^{-a(T-1)}}{e^a - 1}\right)\right]\left(\frac{1}{6}\right)\left(\frac{5}{6}\right)^{T-2}$$
$$- \frac{1}{4}\left[(T-1)(T-2) - \frac{2}{(e^b - 1)}\left[(T-1) - \left(\frac{1 - e^{-b(T-1)}}{1 - e^{-b}}\right)\right]\right]\left(\frac{1}{6}\right)^2\left(\frac{5}{6}\right)^{T-3} \quad (24)$$

See Mathematical model (Technical Appendix) for a full description of Eq. (24) for each group.

Computational simulation

To assess individual learning performance on the basis of time compaction hypothesis, a set of 10^5virtual participants were considered for each experimental group. For each virtual subject, an 80-trials length sequence of random 'stimuli' was generated (a number between 1 and 6 corresponding to one of the six displayed dynamic situations). According to the model's assumption, the response to the first appearance of a given stimulus depends on the previous conditioning: for Control group the answer will always be random, whereas Favoured and Hampered group will always guess right or fail the first appearance of those stimuli corresponding to DMs (dynamic matching situations). For the subsequent trials, the virtual participant will answer according to an exponential recalling process until the learning has been attained, which is assumed at fourth or later appearance of the stimulus. Therefore, the model assumes recalling can only happen in the second and third occurrences of the stimulus, so for these simulation trials, the probabilities of recalling will be respectively:

$$p(\text{recall at } T_2) = e^{-a(T_2-T_1)} \qquad (25)$$

$$p(\text{recall at } T_3) = e^{-b(T_3-T_2)} \qquad (26)$$

where a and b are the recalling decay rates, and T_i stands for the trials in which the i-th appearance of such a stimulus occurs. Following a Monte-Carlo simulation, at each trial $T_{\{2,3\}}$ a random uniform number between 0 and 1 is generated: if it is lower than the recalling probabilities (25) or (26), the virtual subject's answer will be correct; if not, the virtual response will be random. For four or more occurrences of a certain stimulus it is assumed the answer is always correct. This process is repeated for every participant until the learning criteria is fulfilled (18 successes in the last 20 trials).

The pipeline proceeded through the following steps:

1. The sequence of stimuli received during the experiment was identified for each real participant.
2. Since learning length is shorter than the maximum length of stimulus sequence, the sequence was padded with random stimuli until reaching a length equal to 80. Up to 10^3 extended stimulus sequences were generated from the real stimulus sequence per participant.
3. Each extended stimulus sequence was then introduced 10 times into the simulation.
4. Up to 10^6 sequences of possible answers were obtained, leading to 10^6 learning lengths for a single participant.
5. Steps 1 to 4 are repeated for all participants from each group.

Model fitting and experiment simulation were programmed in MATLAB v17 (2017) and R v3.3.1, package *nlstools* (Baty et al., 2015).

3.3. Neuronal model of time compaction

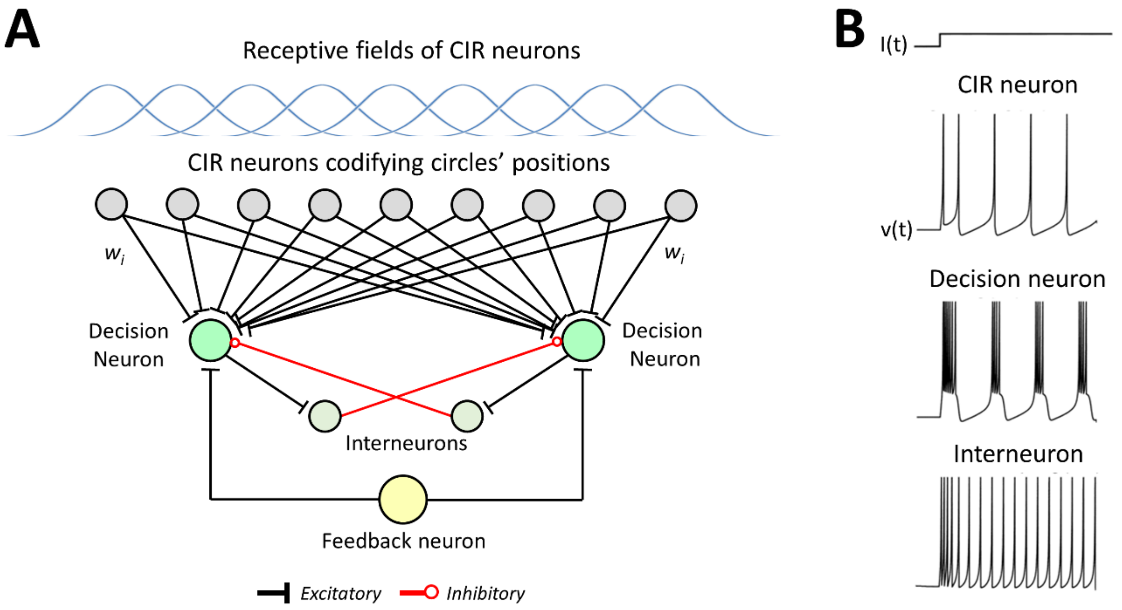

Figure 12. Neural network model. A Schema of network's architecture and layers. Neurons in CIR layer encodes the predicted trajectories of circles in the stimuli. Each CIR neuron sends its excitatory output to both neurons in decision layer. The strength of each synapse is modulated by its weight wj. Decision neurons compete with each other by means of inhibitory interneurons. The feedback node compares the decision output with the true value (i.e. collision/crossing stimuli classified as such or not) and modulates the synaptic weights by an STDP mechanism. **B** Firing patterns of the neuronal types involved in the network, according to combinations of Izhikevich's parameters. I(t) represents a tonic current injection and v(t) corresponds to membrane voltage.

The model simulates the internal process of representation of time-changing situations and decision-making that occurs in the brain, according to time compaction. The proposed neural network is of predictive nature, so it can be understood as the cognitive counterpart to the perception of an actual visual stimuli. The network is set in the context of a two-choice forced task, not unlike the behavioural experiment carried out in humans in the present work. Stimuli fed to the network consist of moving circles arranged either in collision or crossing trajectories, and the network is trained to classify between them. Note that because the network operates at the predictive level, collision here refers to coincidence in the CIR spatial lattice, not physical contact or rebound.

Network structure and functionality

The network is structured in three layers: the CIR layer, a Decision layer and a Feedback Reinforcement layer (Fig. 12A):

- CIR layer is an 41x41 2D layer of neurons with RFs spread across the visual field so their centres were equally distributed in both dimensions. RFs were bivariate normally distributed with means corresponding to their centre of coordinates and the same standard deviation in both dimensions (Mehta et al., 2000). All neurons within the CIR layer send output to all neurons in the decision layer.
- Decision layer is formed by two decision neurons and two local inhibitory neurons, reciprocally innervated. Both decision neurons received input from all neurons in CIR layer and from the feedback reinforcement layer. Decision neurons inhibit each other by means of their corresponding inhibitory neuron. Thus, decision neurons are engaged in a competition and the one with the highest firing rate gets to send its output to the feedback layer (Wei & Bu, 2017).
- Reinforcement layer is formed by a node that receives input from both decision neurons and send them back appropriate positive or negative feedback, depending on whether there is a match between the true hidden rule and the decision taken. Agreement increases the synaptic weights between the winner decision neuron and the CIR layer, whereas disagreement results in synaptic depression. The reinforcement neuron only communicates with the active (winner) decision neuron, so the synaptic weights for the silent decision neuron passively decay with time (Song et al., 2000).

Neuronal components

All neurons within these layers were built as cortical neurons following the Izhikevich model (2003), which comprises two ordinary differential equations:

$$C\frac{dV(t)}{dt} = k(V(t) - v_r)(V(t) - v_t) - u + S(t)$$

$$\frac{du}{dt} = a\{b(V(t) - v_r) - u\}$$

and an auxiliary linear term to reset the voltage after a spiking event to the resting potential:

$$if\ V(t) \geq v_{peak} \Rightarrow V(t) \leftarrow c \qquad u \leftarrow u + d$$

Here, *V(t)* represents the membrane potential, *u* is a membrane recovery variable that provides negative feedback to *V(t)* and accounts for the activation of K^+ currents and inactivation of Na^+ currents, v_r is the membrane resting potential, v_t is the instantaneous threshold potential, S*(t)* refers to the sum of all external currents applied to the neuron and *k* is a scale corrector to adjust *V(t)* units to millivolts and *t* to milliseconds.

The four parameters *a, b, c, d* have different meanings. Parameter *a* is the inverse of the time constant of the *u* recovery dynamics, parameter *b* measures how strongly *u* is coupled to *V(t)* and describes the sensitivity to subthreshold fluctuations of the membrane potential, parameter *c* describes the after-spike reset of the membrane potential caused by fast K^+ conductances, and parameter *d* describes the after-spike reset of the recovery variable by slow K^+ and Na^+ conductances.

According to Izhikevich (2003), different combinations of the aforementioned parameters result in firing patterns typically exhibited by known types of cortical neurons. In the present work, neurons in CIR layer were built as regular spiking neurons (a=0.02, b=0.2, c=-65 and d=8), decision neurons were built as chattering spiking neurons (a=0.02, b=0.2, c=-50 and d=2) and interneurons within the decision layer as low threshold spiking neurons (a=0.02, b=0.25, c=-65 and d=2) (Fig. 12B). The remaining parameters were common for all neurons so capacitance, *C*, was set to 50, v_r to -60, v_t to -45 and v_{peak} to 40. For stability, *dV(t)* was evaluated twice at *dt*/2 time steps.

Synaptic junctions

All synapses were modelled by means of an alpha function, so each spiking event changes the synaptic conductance over time on the postsynaptic neuron according to:

$$g_s(t) = g_{max}\frac{t - t_0}{\tau_s}e^{1-\frac{t-t_0}{\tau_s}}$$

Where g_{max} is the maximum synaptic conductance, τ_s is the time constant of the synapse and t_0 is the time at which the trigger spike appeared. At a certain time *t* the total conductance of the i-th synapse is:

$$G_s(t)_i = \sum_{sp-1}^{Nsp} g_s(t)_{i,sp}$$

Where $g_s(t)_{i,sp}$ is the conductance of the i-th synapse at time *t* due to the sp-th spike and *Nsp* is the number of spikes that reached the synapse.

The injected current due to synaptic conductance was added to de *S(t)* term of the Izhikevich expression as:

$$I_s(t)_i = w(t)_i\, G_s(t)_i\, \big(E_s - V(t)\big)$$

Where $I_s(t)_i$ is the current due to the conductance of the i-th synapse at time t, $w(t)_i$ is the weight of the i-th synapse and E_s is the reversal potential.

Synapses from CIR neurons to decision neurons and from decision neurons to interneurons were excitatory ($E_{ex} = 50$, $g_{ex} = 5$ and $\tau_{ex} = 2$), following Na$^+$ equilibrium potential; whereas the reciprocal synapsis from interneurons to decision neurons were inhibitory ($E_{in} = -90$, $g_{in} = 2.5$and $\tau_{in} = 2$), following K$^+$ equilibrium potential.

Synaptic plasticity

Synaptic plasticity was modelled reflecting the activity patterns required to induce changes in synaptic weights, according to an STDP paradigm (Gerstner et al., 1996; Song et al., 2000). Learning process only affected synapsis between neurons in CIR layer and active decision neurons. When excitatory synapse a between CIR layer and decision neuron is active and a presynaptic spike reaches the decision neuron from the reinforcement layer (positive feedback), then

$$g_{ex}(t) \rightarrow g_{ex}(t) + \bar{g}_a$$

Where the peak conductance $\bar{g}_a$ reflects the change in synaptic weights, as conductance is fixed and scored by a weight value ranging from 0 to 1, so $g_{max} = 1$. Otherwise, synaptic conductances decay exponentially,

$$\tau_{ex} \frac{dg_{ex}}{dt} = -g_{ex}$$

Synaptic modification is generated in the model through $N + 1$ functions, $M(t)$ and $P_a(t)$, for $a = 1,2,\ldots,N$. $M(t)$ is used to decrease synaptic strength, whereas $P_a(t)$ is used to increase the strength of synapse a. These decay exponentially,

$$\tau_{-} \frac{dM}{dt} = -M \quad \text{and} \quad \tau_{+} \frac{dP_a}{dt} = -P_a$$

Whenever there is a presynaptic spike at synapse a and time t, $P_a(t)$ is incremented by an amount A_+,

$$P_a(t) \rightarrow P_a(t) + A_+$$

$$g_a \rightarrow g_a + M(t)$$

$$if\ g_a < 0 \rightarrow g_a = 0$$

Whenever there is a postsynaptic spike at time t, $M(t)$is decremented by an amount A_-,

$$M(t) \rightarrow M(t) + A_{-}$$

$$g_a \rightarrow g_a + P_a(t)$$

$$if\ g_a > 1 \rightarrow g_a = 1$$

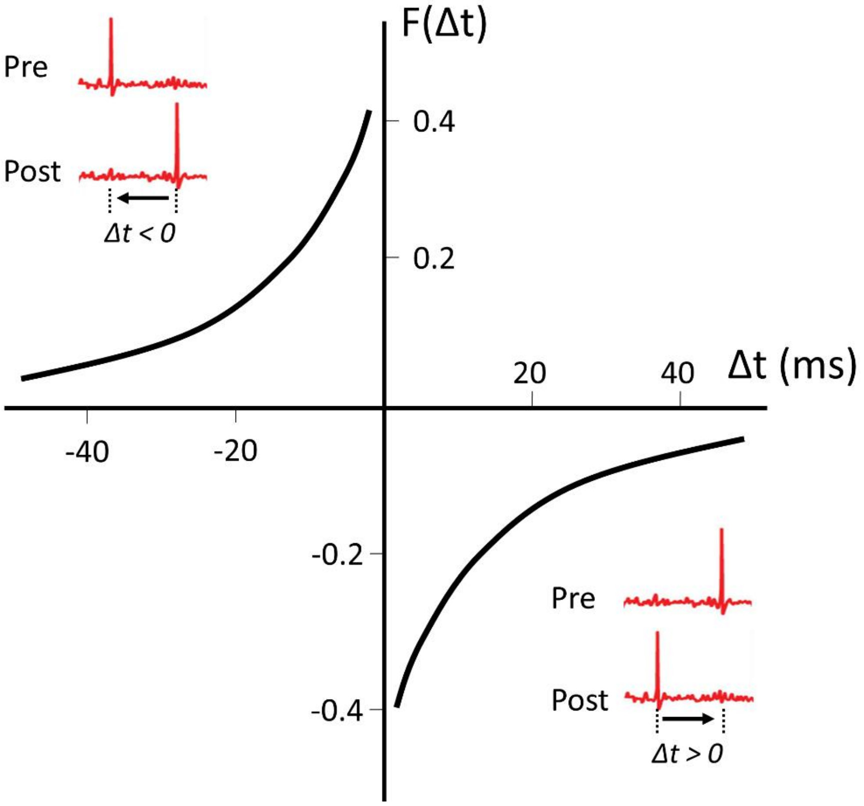

Figure 13. STDP mechanism. F(Δt) represents synaptic change and Δt is the time of the presynaptic spike minus the time of the postsynaptic spike. The change of the peak conductance at a synapse after a given pre- and postsynaptic action potential pair is F(Δt) times the maximum conductance value g_{max}. A pre-synaptic spike followed by a post-synaptic one leads to synapse potentiation (up to 50 ms), whereas a post-synaptic spike preceding a pre-synaptic resulted in synapse depression. In this figure, F is expressed as a percentage. Thus, a value A+ = 0.005 would correspond to a change of 0.5% of the maximum synaptic strength per spike pair. If the peak synaptic conductance is modified beyond the allowed range $0 \leq g_a \leq g_{max}$, g_a is set to the corresponding limiting value. Adapted from Song et al. (2000).

A graphical summary can be seen in Figure 13. For the current experiments, decay rate A_{+} was set to 0.005 and learning rate A_{-} to 0.5 (arbitrary units).

Stimuli generation

Stimuli consisted of two circles moving in vertical and horizontal trajectories with equal velocities. Circles in collision trajectories entered the network at the same time and collided at the centre coordinates, whereas crossing stimuli were defined in terms of offset from the collision positions (i.e. collision corresponds to offset = 0), so their initial positions didn't match.

Preplay reconstruction of moving circles was simulated by transforming spatial RFs of neurons in CIR layer into temporal RFs, using circles velocities in each direction. Neurons received a current of variable intensity over time, which emulates predictive preplay of the stimuli's trajectories by sequential activation of RFs in the CIR layer. All neurons in CIR layer received a synchronous sinusoidal current injection corresponding to theta rhythm activity, so the spikes evoked in a theta cycle constituted the input to neurons in the decision layer.

For the experiments in this work, circles' velocity was set to 0.003, current intensity was set to 1500 (200 for low intensity stimuli) and collision initial positions were (26,26), with respect to the 41x41 matrix representing CIR layer (arbitrary units).

4. RESULTS

4.1. Evidence of time compaction in human brain

Existence of time compaction

261 participants (135 women and 126 men) were engaged and randomly distributed between Control, Favoured and Hampered groups, and an additional 92 participants (50 women and 42 men) were assigned to a Validation group, meant to assess experimental assumptions. In a first phase, participants had to classify the static stimuli and uncover the hidden rule 1. In a second phase, they had to classify the dynamic stimuli to reveal the hidden rule 2.

Population learning performance was analysed by fitting the success rate to logistic regressions. Among all the independent variables tested (trial, gender, group, and researcher), only gender and group factors were found significant. Fig. 14A shows the success rate per trial, independently for men, women and different experimental groups. In accordance with time compaction's predictions, population learning in men was significantly modulated for Favoured and Hampered groups compared to Control. Men in Favoured group learnt at a faster rate than Control, whereas men in Hampered group learnt at a slower rate. Surprisingly, no significant differences were found for women. Moreover, their performance was comparable to men in the Control group.

To characterize the individual learning performance, the learning length of each participant was appraised through the number of trials required to figure out hidden rule 2 (Fig. 14B). Men from Favoured group had significantly higher probability of learning compared Control men, whereas men in Hampered group showed lower learning probability (Fig. 14B, inset). On the contrary, phase 1 did not affect individual learning in women. Yet, no significant difference was found for all groups of women against men in the Control group.

These outcomes reveal an intrinsic cognitive relationship between SM and DM stimuli suggesting that men internally represent dynamic situations mainly by the static representation of relevant interactions. The lesser salience of time compaction in women and the absence of differences against the Control group of men reflect that women might be relying on time compaction alongside a broad range of alternative decision-making strategies, as has been stated in other studies (Peña et al., 2008; Picucci et al., 2011).

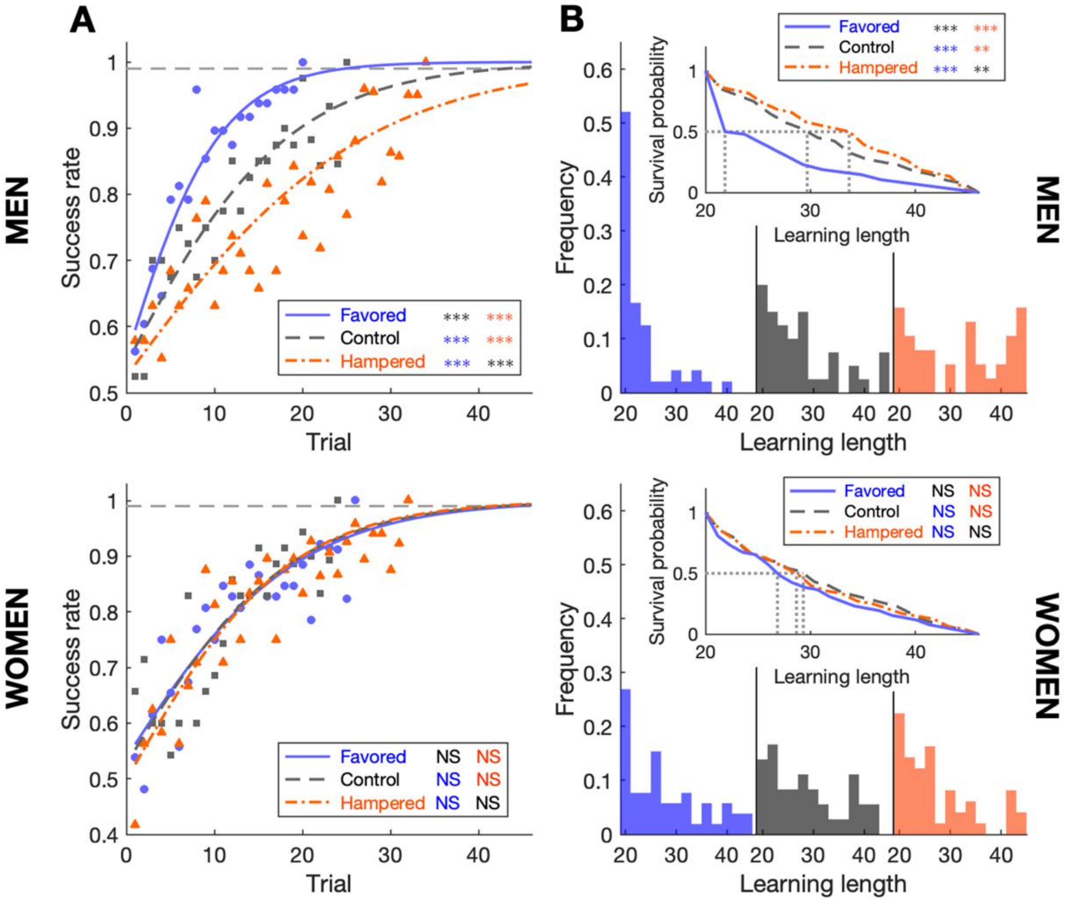

Figure 14. Modulation of learning performance in phase 2. Blue, black, and red colors stand for Favored (F), Control (C), and Hampered (H) groups (F: 48 men, 52 women; C: 40 men, 35 women; H: 38 men, 48 women). Top and bottom rows correspond to men and women, respectively. **A** *Population learning process as success rate per trial* (considered up to 0.99 level, dashed lines). Curves describe the logistic regression of the corresponding population learning process. Men in Favored group learned the hidden association rule faster than men in Control and Hampered groups (F vs. C: *p* = 3e-04; F vs. H: *p* = 9.8e-13), and conversely men in Hampered group found out the association rule at a slower rate than Control group (C vs. H: *p* = 2.5e-04). Population learning process in women showed no differences regarding the experimental group (F vs. C: *p* = 0.43; F vs. H: *p* = 0.28; C vs. H: *p* = 0.93). Men from the Control group and women from all groups showed no significant differences (*p* = 0.23, n = 40 vs. 135). **B** *Individual learning performance*. Histograms show distribution of learning lengths. There is an increased likelihood for men in Favoured group to discover the hidden rule in contrast to Control and Hampered groups (F vs. C: *p* = 7.2e-04; F vs. H: *p* = 3.5e-8), whereas men in Hampered group were less likely to find out the hidden rule than Control group (C vs. H: *p* = 5.8e-03). This effect was not observed in women (F vs. C: *p* = 0.98; F vs. H: *p* = 0.67; C vs. H: *p* = 0.76). Men from the Control group and women from all groups did not show significant differences (*p* = 0.95, n = 40 vs. 135). Insets show Cox survival curves quantifying differences in the individual learning performance. Dotted lines mark the learning length for a 0.5 learning probability. ***: < 0.001; **: < 0.01; *: < 0.05; NS: No significant difference. Data from Villacorta-Atienza et al. (2021).

Salience of time compaction

As shown above, the previous exposure to phase 1 alters the learning performance in phase 2. Below a detailed explanation of how the process might occur is provided.

Fig. 15A shows a typical random sequence of dynamic stimuli. Learning hidden rule 2 encompasses two opposite mechanisms, (1) the information accumulation with each trial expedites the association rule's discovery, and (2) the distance (number of trials) amid consecutive appearances of a stimulus promotes the forgetting of the previously established associations. It can be presumed that under the control setting (no previous information is available), a subject gives a random answer to the first presentation of a given stimulus (e.g. DM at trial 3). As the task is dichotomous (up/down), if the pressed key is wrong, the opposite one must be right, so the participant may always deduce the correct association. Then, in the second apparition of the same stimuli (e.g. DM at trial 7, after four trials), the three intermediate stimuli

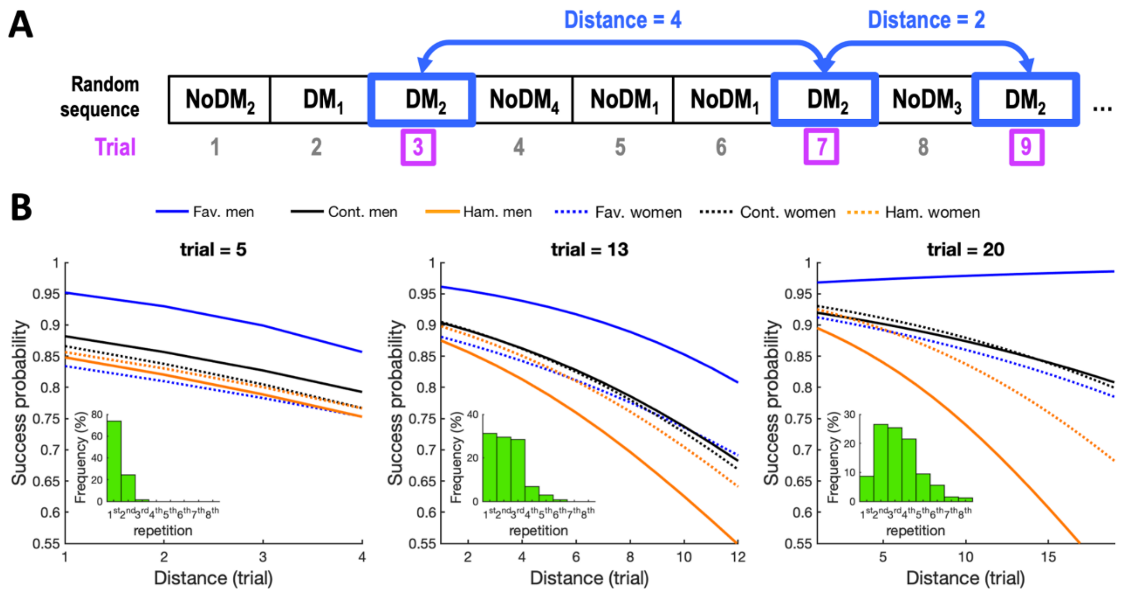

Figure 15. Salience of time compaction within phase 2. Distances between successive appearances of a given stimulus influence its learning. **A** Example of a sequence with six dynamic stimuli (two DMs and four non-DMs) in phase 2. In the example, DM2 appears at trial 3 for the first time, at trial 7 for the second time (distance in trials = 4), and lastly at trial 9 (distance = 2). **B** Population probability of successful answer at the next appearance of DM stimulus for different groups of subjects at the beginning of the learning process (trial 5), at the intermediate stage of learning (trial 13), and at the final stage (trial 20). Insets show the frequency distribution of repetitions of the stimuli in a sequence as the one in (A). Solid and dashed colored curves depict the success probability fitted by logistic regression (GLM, logit link). The repetition distance and trial association differ significantly between experimental groups for men (between distance, trial and group p = 5e-4; pairwise distance and trial for Favored group p = 1e-4, for Control Group p = 0.028 and for Hampered group p = 1e-3) but not for women (between distance, trial and group p = 0.08; pairwise distance and trial for Favored group p = 0.06, for Control Group p = 0.54 and for Hampered group p = 0.92). Data from Villacorta-Atienza et al. (2021).

will interfere in the recalling of the association discovered at the first apparition. In this sense, time compaction predicts that phase 1 should affect the forgetting rate of associations learned within phase 2. This claim is explored here by analysing the probability of successful answers as a function of the distance between stimulus appearances and the trial number, which is done for the three experimental groups. Fig. 15B summarizes the population results.

As there were 6 possible stimuli in phase 2, at trial 5 the majority of stimuli were repeated only once (Fig. 15B, left, inset), and hence learning has barely begun. When the same stimulus is repeated within a short interval (distance < 5), probability of a successful answer is higher (> 0.75) in all groups of subjects (Fig. 15B, left), and particularly for participants in the Favoured group across all distances. The latter supports time compaction since, according to this hypothesis, participants from the Favoured group should have acquired CIR knowledge previously in phase 1, thereby answering phase 2 correctly.

Most of the stimuli have been repeated 1 to 3 times at trial 13 (Fig. 15B, middle, inset). At this point in the learning process, the curve for Favoured participants appears less affected by distance, so these subjects are more resilient to forget the learned associations than Control participants, as predicted by time compaction. For the Hampered to Control comparison, distance has a greater effect on the learning process, making them more prone to forgetfulness. Lastly, trial 20 characterizes the final learning stage, showing the already discussed differences in learning.

Therefore, this analysis suggests two mechanisms are engaged in learning modulation throughout the experiments: prior information and individual resilience to forgetfulness. Both show compatibility with the connection between phases 1 and 2 hypothesized by time compaction.

Rule verbalization corroborates gender-wise salience of time compaction

To explore to what extent time compaction is manifested at conscious level, participants were requested to verbalize the hidden rule 2 they identified in phase 2. Written answers were analysed and labelled into two categories, ‘‘collision-related” (i.e., CIR related) and ‘‘others”. Fig. 16A shows the probability of ‘‘collision-related” responses as a function of the learning length. Generalized linear modelling with logit link function revealed that fast-learning men show a significant propensity of answering in terms of a ‘‘collision” despite the experimental group.

Moreover, men who required more trials to learn also resorted more frequently to alternative strategies based on other criteria, such as circles’ velocities. Such tendency was not evident among women, who responded in terms of a collision regardless of the learning length and practically at chance level (45%). That is particularly meaningful for the groups of participants with learning length within [40,46] trials, where women identified the correct ‘‘collision rule” more often than men. This finding further supports the conclusion stated above regarding the broader range of decision-making strategies women may apply.

So far, the effect of phase 1 over phase 2 has been observed both at levels of population and individual learning performance. To explore the possibility that these differences could also be explained due to variable difficulty inherent to the association task, response times were studied (i.e. elapsed time between stimulus disappearance from screen and the keyboard arrow is pressed). Fig. 16B shows that no significant differences regarding the experimental group were found for either women or men. This suggests that every participant had the same difficulties in undertaking the test irrespective of their prior conditions. This conclusion is consistent with the findings discussed previously, thereby reinforcing the idea that observed differences result from the information management during phase 2 more than from task difficulty alterations.

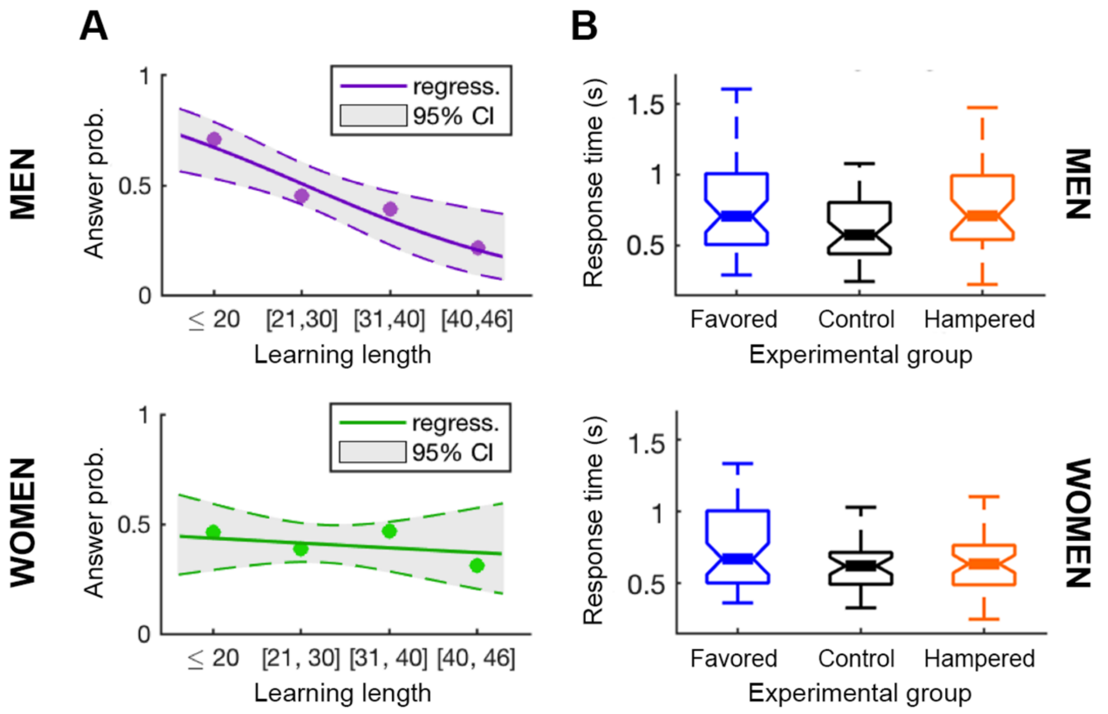

Figure 16. Rule verbalization and response time. A Men who quickly learned the rule were more prone to verbalize it in terms of “collision”, regardless of the experimental group. The probability decreases with the learning length. No correlation is observed for women (thick curves and grey areas denote logistic regression and confidence intervals at 95%, respectively; men: p = 1.2e-3, n = 126; women: p = 0.67, n = 135). **B** Response time shows no differences among groups (GEE with linear link function, F vs. C: p = 0.13, n = 100 vs. 75; F vs. H: p = 0.45, n = 100 vs. 86; C vs. H: p = 0.42, n = 86 vs. 75) and for gender (p = 0.4, n = 126 men vs. 135 women). Data from Villacorta-Atienza et al. (2021).

Technical validation of the experimental task

In order to assess the complexity of the task, let consider the trial where all different stimuli (three scenes in phase 1 and six situations in phase 2) have repeated once (i.e. have appeared twice). Frequency distribution of this 1st repetition trial for three and six different stimuli (for phases 1 and 2 respectively) is shown in Figure 17A. Dotted lines denote the interval containing the 90% of the probability of having all stimuli repeated once: [6, 13] for phase 1 and [12, 33] for phase 2.

Since phase 2 is more difficult than phase 1 (six vs. three stimuli to be classified), its complexity will define the complexity of the proposed task. This way, for phase 2, in the 90% of random sequences composed of 33 stimuli or less, all stimuli will repeat once, so they would allow the learning of the association rule under the assumption of 'perfect recall'. This conclusion is compatible with the expected stimulus length required to learn the rule: if the expected repetition distance is 6 and all the six different dynamic stimuli must repeat at least once, the estimated stimulus length for rule learning will be 36. Therefore, it can be concluded that, in the conditions of the Control group and being conservative, it would be reasonable to expect an average learning length of 30 trials during phase 2.

Additionally, the influence of specific sequences of stimuli that might be hindering the learning performance by chance is monitored here through an index of sequence difficulty, *D(s)*. The index strongly depends on the distance between repetitions of a given stimulus and is normalized to make sequences with variable lengths comparable. This way, a sequence $s_1 =$

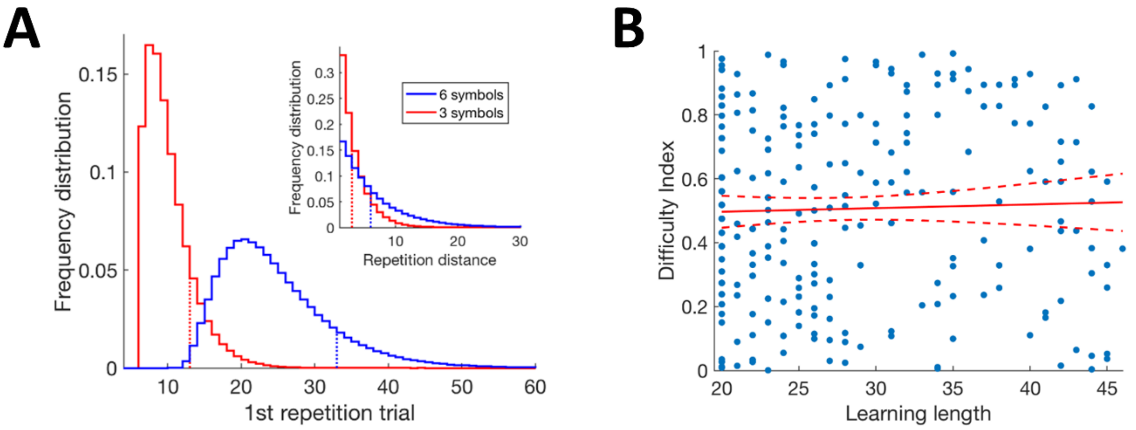

Figure 17. Technical validation of experimental procedure. A Frequency distribution of the first trial where all stimuli appeared repeated once. Dotted line denotes the interval of 1st repetition trials with probability equal to 0.9. *Inset.* Frequency distribution of repetition distance and expected repetition distance (dotted line). Red and blue lines stand for stimuli with three scenes (phase 1) and six situations (phase 2). **B** No significant correlation is observed in the functional sample between stimulus difficulty index and learning length. *p-value* = 0.63.

[1 1 1 1 1 1 1 1] will have lower difficulty (D(s) = 7.69) than a sequence $s_2 = [1\ 2\ 3\ 4\ 1\ 2\ 3\ 4]$ (D(s) = 18.77). Plotting *D(s)* against learning length for Control group reveals that there is no influence of the sequence structure over experiment performance, since no significant correlation exists (Fig. 17B). This analysis corroborates that participants were not biased by the random properties of the experimental task, since neither complexity nor sequence of stimuli affected the learning performance.

Individual performance stability

Based on the stimulus difficulty evaluation, it can be safely assumed that any participant in our experiment had enough ability to successfully carry it on. Moreover, all participants performed phase 1 at comparable levels, regardless of gender and the experimental group (Fig. 18). Thus, ability can be considered a fixed feature across the subjects that reduces the outcome variability to the motivation dimension. Therefore, it is reasonable to divide the sample between motivated individuals, who correctly performed the task showing a stable performance, and unmotivated individuals, who did not. A potential indicator of this latter group is the appearance of a sample fraction (18%) that does not fit for proportional hazards between experiment and gender in the Cox model, which in addition corresponds to participants with learning lengths greater than 46 (Fig. 19).

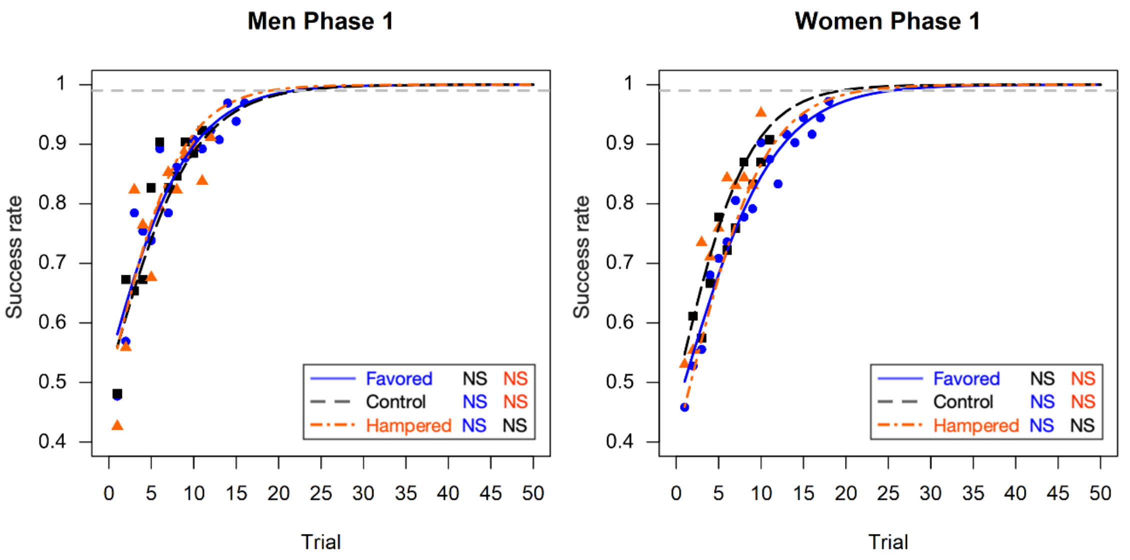

Figure 18. Learning performance in phase 1. Blue, black, and red colors stand for Favored (F), Control (C), and Hampered (H) groups respectively (F: 48 men, 52 women; C: 40 men, 35 women; H: 38 men, 48 women). Population learning process showed no differences between experimental groups, neither for men (F vs. C: $p = 0.545$; F vs. H: $p = 0.45$; C vs. H: $p = 0.48$) nor for women (F vs. C: $p = 0.25$; F vs. H: $p = 0.11$; C vs. H: $p = 0.32$). Men from the Control group and women from all groups showed no significant differences ($p = 0.28$, n = 40 vs. 135). Curves describe the logistic regression of the corresponding population learning process. ***: < 0.001; **: < 0.01; *: < 0.05; NS: No significant difference.

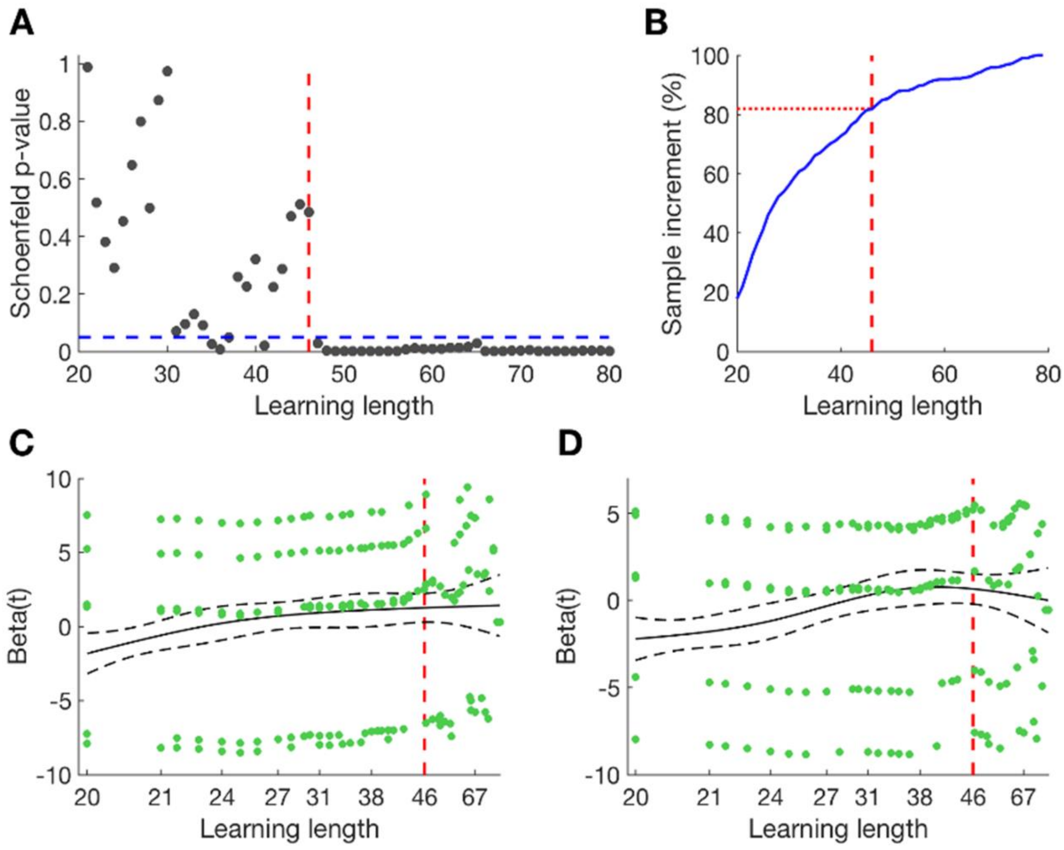

Figure 19. Proportional hazard ratio model assumptions. A Schoenfeld test always rejects Cox assumptions satisfaction hypothesis (proportional hazard assumption) when considering individuals with learning length > 46 (blue dashed line at 0.05 and red dashed line at 46). The drop at learning length = 30 wasn't accompanied by significant alterations in the scaled residuals shown in D. **B** Smooth increment in sample size from learning length equal to 46 shows that the sudden drop in the Schoenfeld p-value is not caused by sampling in the Schoenfeld test (82% of the sample corresponds to learning lengths ≤ 46). **C** and **D**. Scaled Schoenfeld residuals against transformed time. Beta(t) stands for regression coefficients of interactions terms between gender (panel C/D for men/women) and experiment factors. The diagnostic plots show a fitted spline of 4 degrees of freedom (solid line) and a 95% confidence interval (dashed lines). The parallel structure expected from the proportional hazard assumption is lost for learning lengths greater than 46, indicating violation of non-proportionality from this value.

In view of these results, the performance stability of each participant is explored here in more depth. This procedure was meant to assess the existence of a 'demotivated' group, as pointed by the collapse of the proportional hazard assumption. In a trial-error procedure, when a certain stimulus appears for the first time the subject must randomly respond, so success probability to the first appearance is 0.5. In this context, if the same stimulus is repeated immediately after this first appearance (i.e. at the next trial) the subject will always guess the correct answer. Thus, success probability for the first repetition would be 1. However, if this first repetition occurs at a certain distance from the first occurrence (in number of trials), its success probability could be affected by various factors, such as distraction, forgetting, etc. The same can be applied to the following repetitions of the stimulus. Only the first two repetitions are used here, since, according to the simplicity of the task, a participant who is properly performing the task should have achieved a high learning rate at this moment. The success frequency $f_i(d)$ of the entire sample at each repetition distance d was calculated taking the six stimuli together, where i =1, 2 stand for the first and second repetition respectively. For each subject its *response* probability to the stimulus j which appears at a distance t_j, from its previous appearance, $rp_{i,j}$, will be $f_i(t_j)$ if he responded correctly and 1-$f_i(t_j)$ if he failed. This way, the *repetition* probability rp_i for each individual will be:

$$rp_i = \prod_{j=1}^{6} rp_{i,j}$$

assuming the independence of each response to a certain stimulus. If a subject is performing the task properly, high probabilities of at least one repetition will be expected. On the contrary a subject not responding properly will have 1st and 2nd repetition probabilities around or lower than 0.56, the expected value for random answer probabilities. Density plot of 1st vs. 2nd repetition probabilities shown in Figure 20 corroborates previous Cox regression analysis, displaying highest density of subjects with learning lengths ≤ 46 in good-performance areas whereas subjects with learning lengths > 46 corresponds to people who are not correctly performing the task. The detailed distribution of these two populations according to experimental group and gender shows that most subjects with learning lengths ≤ 46 had at least either the 1st or the 2nd repetition probabilities above randomness (Fig. 21), while subjects with learning lengths > 46 lie around randomness (Fig. 22).

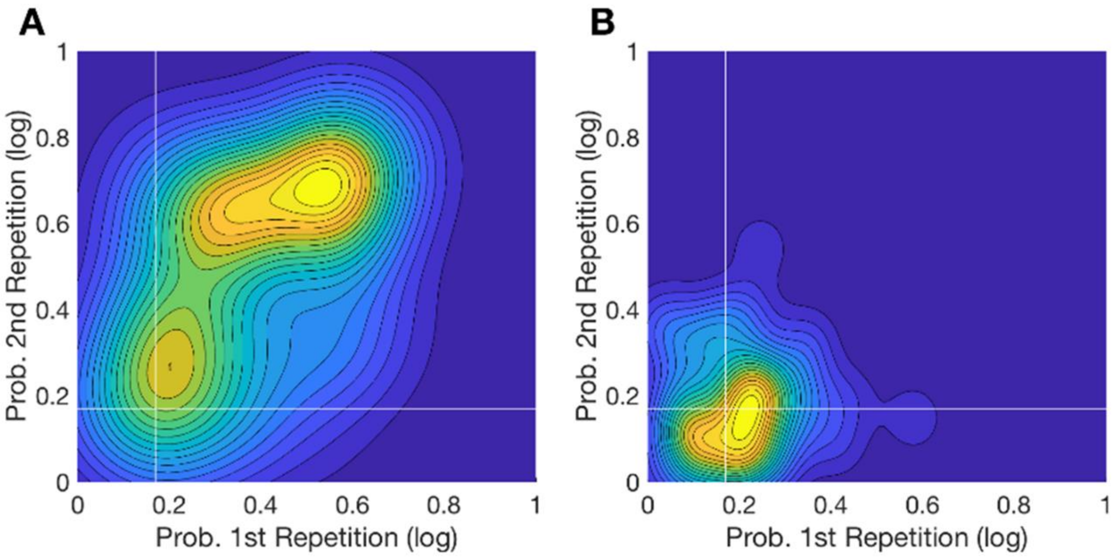

Figure 20. Density plot of repetition probability. A Density plot of 1^{st} vs. 2^{nd} repetition probabilities for subjects with learning lengths ≤ 46 and **B** for subjects with learning lengths > 46. Vertical and horizontal scales are logarithmic: $\log(1+\sqrt{probability})$. White vertical and horizontal lines represent repetition probabilities for random answer.

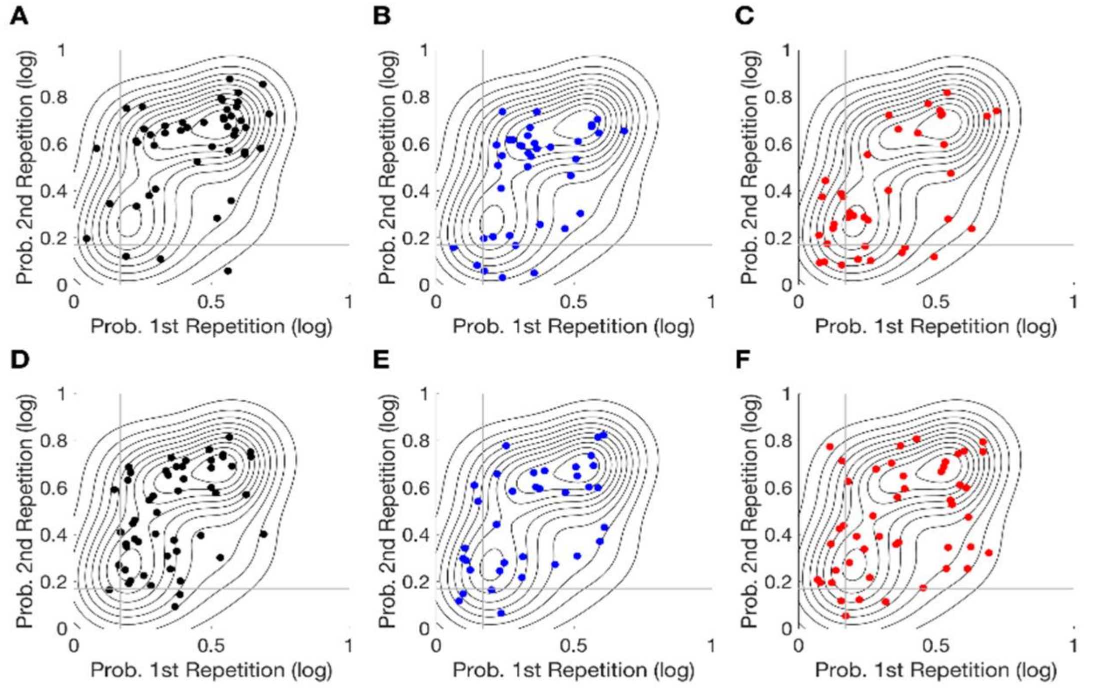

Figure 21. Distribution of repetition probability according to experiment and gender for Learning Length <= 46. A, **B**, and **C** Distribution for Favored, Control, and Hampered men respectively. **D**, **E**, and **F** Distribution for Favored, Control, and Hampered women respectively.

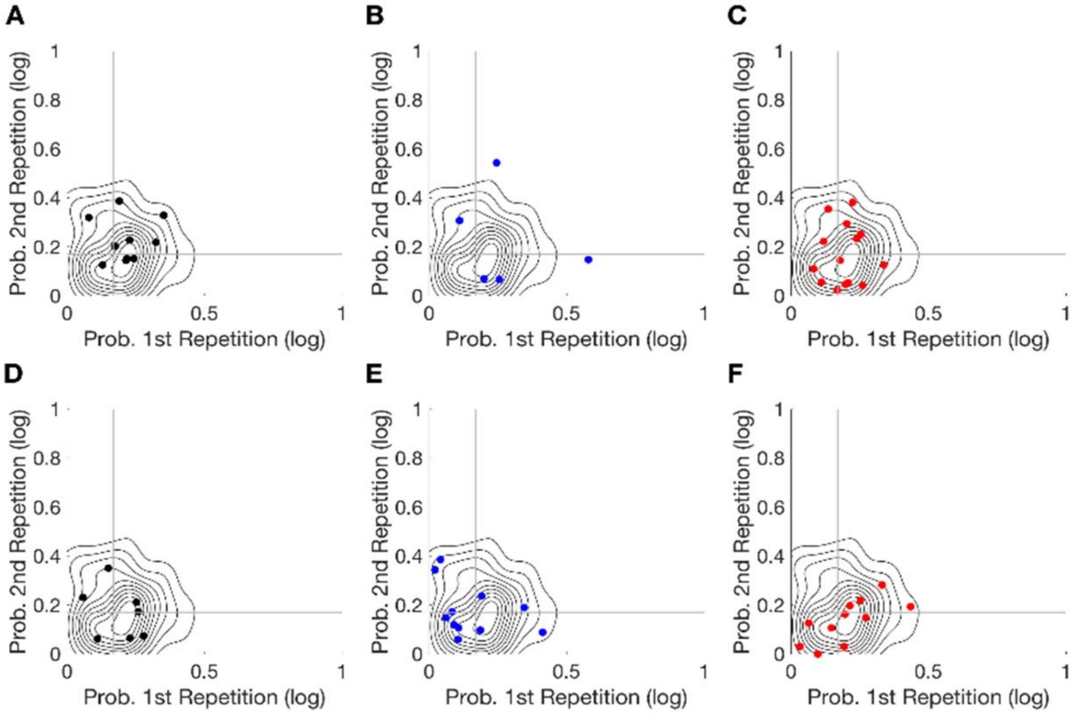

Figure 22. Distribution of repetition probability according to group and gender for Learning Length > 46. A, **B**, and **C** Distribution for Favored, Control, and Hampered men respectively. **D**, **E**, and **F** Distribution for Favored, Control, and Hampered women respectively.

Putting together Cox regression analysis and repetition probabilities, it seems that two populations characterized by their performance during phase 2 exist. This shows that those participants with learning length below or equal to 46 exhibit a stable performance, which ensures an adequate and valid realization of the experiment.

No crosstalk due to stimulus–response compatibility (SRC)

SRC is one of the most ubiquitous sources of information transfer (Kornblum et al., 1990), and hence a possible explanation to the connection between phases 1 and 2. The question addressed here would be how much of the response can be inferred from the stimulus. Stimuli used in the experiments contain spatial information susceptible to be shared with the response, i.e., the circles' position on screen and the keyboard buttons. For the experiments, vertical-arrow keys were chosen to minimize potential bias due to various reasons: (1) this election facilitates the use of the same hand for pressing the keys, preventing using both hands (in case the selected keys would have been far apart) and so a bias due to the better use of a certain hand against other one; (2) the use of lateral-arrow keys was avoided to prevent lateral bias, potentially induced by the handedness, the writing and reading direction, etc. (Maass et al., 2014); (3) despite different vertical letter keys could be selected, that option was discarded since the letters could carry meanings that could induce unexpected bias; (4) numbers are laterally arranged except for the numeric pad, which is not available in all keyboards.

Up and down arrow keys were counterbalanced to avoid any information transfer between the up-arrow key and the movement direction or top position of the circles, which were randomly assigned for each participant. Furthermore, to discard any crosstalk, the influence that the assignment of the up- or down-arrow could potentially have on the learning performance was explored. The analysis revealed that the key assignment explains no variability across gender and experimental group in terms of the learning length (Fig. 23A). One of the main signatures of SRC is the alteration of the response time, i.e., the time the participant takes to relate the stimulus with the response. No such bias was found between experimental groups in relation to the key assignment (Fig. 23B). This points SRC as an unlikely source of crosstalk that could explain the obtained results.

Validation group discards gender bias

The arguments mentioned above suggest that alternative mechanisms that could be involved in the processing of dynamic stimuli cannot explain the reported gender differences. Nevertheless, to discard any inherent factors to the dynamic stimuli that could not have been considered here, a Validation group consisting of additional 92 subjects (50 women and 42 men) was sampled. The participants of this group skipped phase 1 and took part in phase 2 only.

Population and individual learning performances were analysed in the same way as the experimental groups. The results depict no gender bias during the classification of the dynamic stimuli (Fig. 24). Therefore, phase 2 can be discarded as the source of the observed sex bias. This confirms that learning differences between men and women arise when phase 2 is preceded by phase 1, which supports time compaction as the most likely explanation to the results.

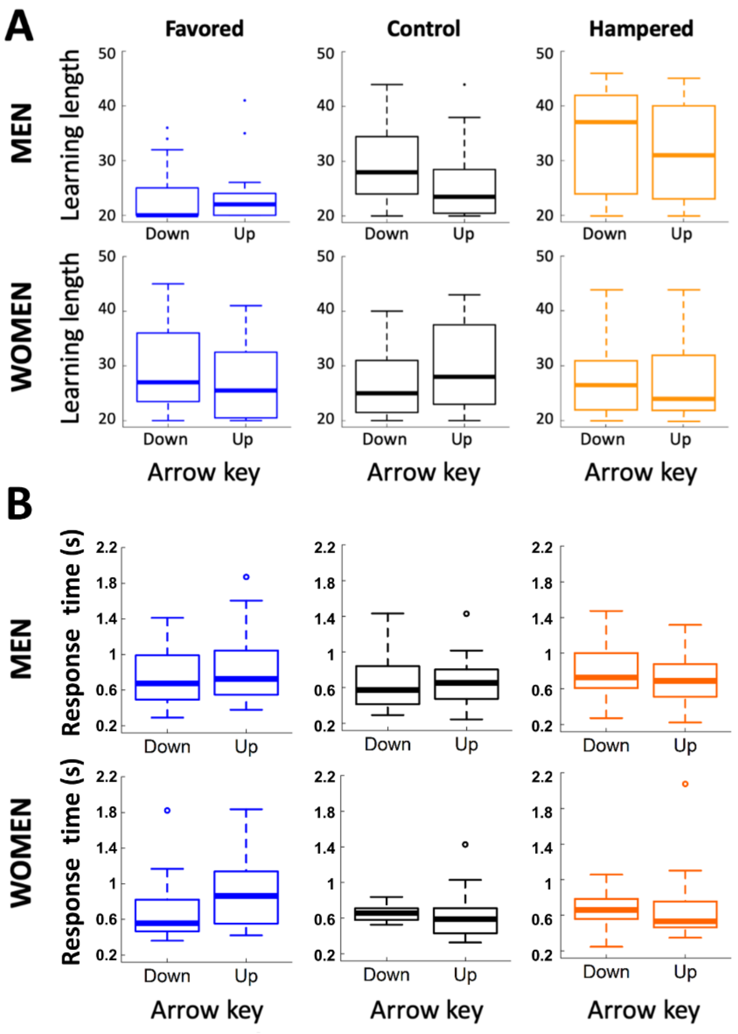

Figure 23. Exploration of SRC. Influence of arrow keys (down and up) on the learning length. **A** All associations are not significant (between gender, experimental group, and arrow key p = 0.17; pairwise interactions gender and arrow key: p = 0.91 for men, p = 0.29 for women; group and arrow key: p = 0.23 for Favored, p = 0.34 for Control, and p = 0.76 for Hampered). **B** Arrow key association doesn't modulate differences in response time. Association between gender, experimental group and arrow key wasn't significant (p = 0.31), nor were any of the pairwise interactions between gender and arrow key (p = 0.64 for men and p = 0.21 for women) or group and arrow key (p = 0.09 for Favored, p = 0.46 for Control, p = 0.57 for Hampered).

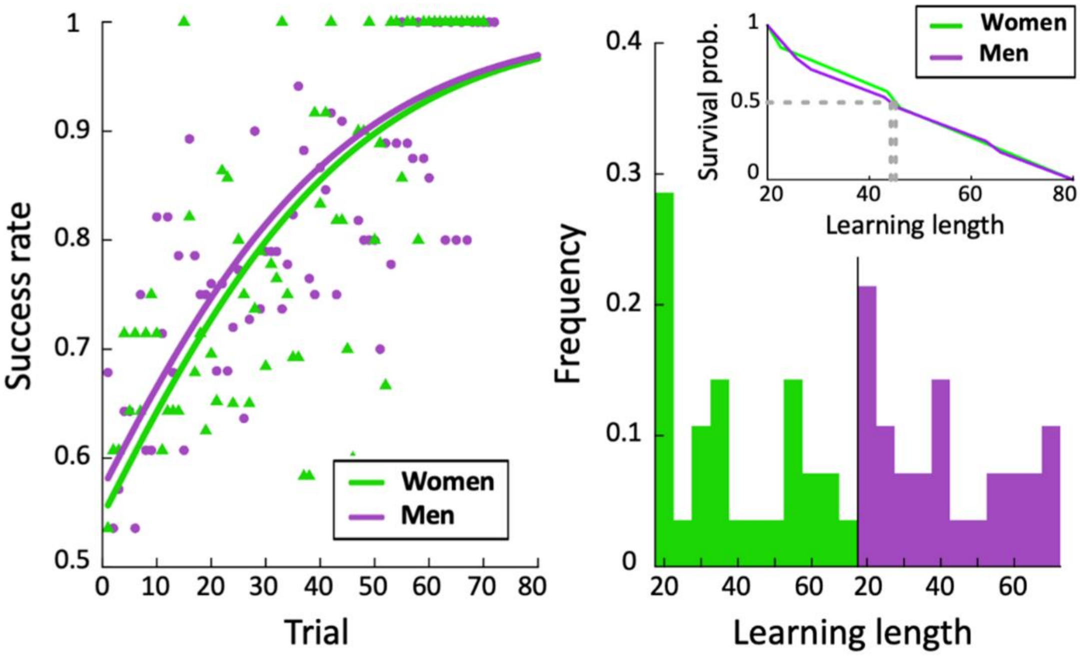

Figure 24. Learning in phase 2 without previous exposure to phase 1. No significant differences between women (green) and men (purple) were found in population (left, p = 0.59) and individual (right, p = 0.48) learning performances. Data from Villacorta-Atienza et al. (2021).

Time compaction is not a salient strategy in children

All the experiments described above were performed on adult human participants. The question of whether time compaction is a cognitive mechanism exploited since childhood or there is an age onset is tackled here. To this extent, 368 children (188 girls and 180 boys) ranging from 9 to 12 years old were engaged to participate in the same experimental setup already described for adults. Whereas phase 1 remained identical, phase 2 was limited from the original six to four stimuli (left and right DM, and left and right non-DM with fast red circle). This change was meant to avoid excessive load of information, taking into account the differences in memory and attentional span between children and adults. For the same reason, experimental groups were also reduced to Favoured and Control conditions, leaving the Hampered condition out due to the additional labour of re-learning that it required.

A logistic regression of the population learning performance found no significant differences due to age, gender or experimental group (Fig. 25A). A close comparison between phases of the experiment revealed that phase 2 was learned at a faster rate than phase 1 (Fig. 25B). Moreover, not all children were capable of solving phase 1, and those who did were able to find the hidden rule in phase 2 faster than children who didn't, regardless of age and gender (Fig. 26A, left plot). This was also evidenced at the level of individual learning lengths (Fig. 26A, histograms). These results lead to the conclusion that phase 1 and phase 2 were not connected by means of time compaction, although there seemed to be a carryover from one phase to the next in terms of ability to perform the game (i.e. game mechanism is learnt in phase 1 which in turn facilitated performance in phase 2). This effect was not modulated by age and gender in any case.

To discard difficulty as a confounding factor, learning performance of phase 1 from children who solved it and phase 2 from children who didn't solve phase 1 were compared (Fig. 26B). The rationale behind this assessment was that there shouldn't be a carryover effect favouring phase 2 performance in children unable to finish phase 1, rendering its phase 2 comparable to phase 1 for children who solved it, in terms of novelty and ability. This comparison yielded no significant differences, which can be interpreted as both phases sharing similar levels of difficulty. Although indirectly, this can be seen as a secondary effect of time compaction strategy yet in maturation, which renders dynamic situations equivalent to static scenarios in terms of allocation of cognitive resources.

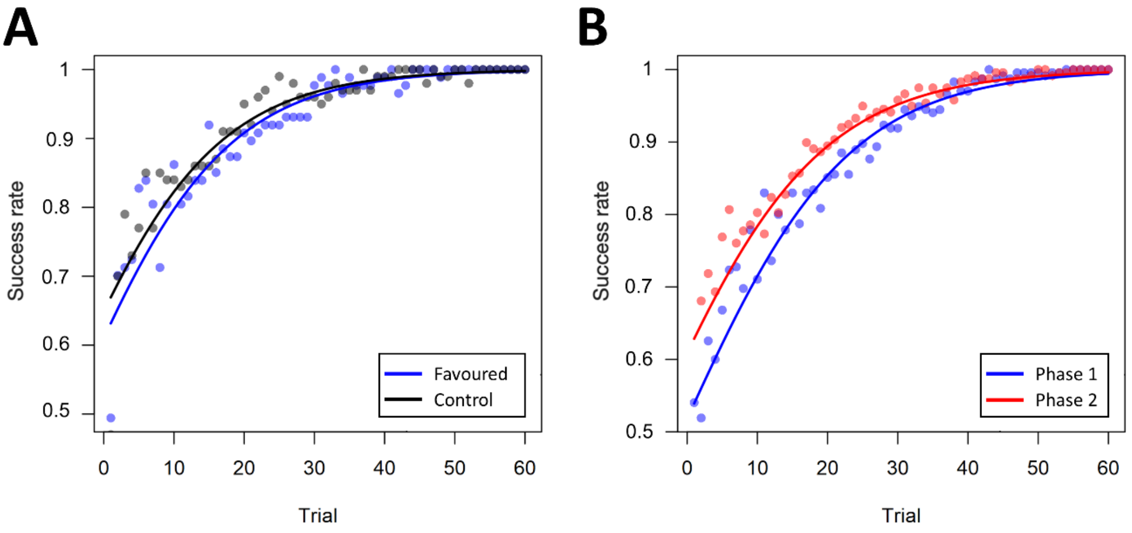

Figure 25. Learning performance in children. Curves represent population learning performance in phase 2. Only children that solved both phase 1 and 2 were included in the comparisons. **A** Blue and black curves represent Favoured (N=94) and Control (N=107) groups. No significant differences were found between phase 2 of Favoured and Control groups (p = 0.52), regardless of age and gender. **B** Phase 2 is learned at a faster rate than phase 1, regardless of age and gender (p = 1e-4, N = 252).

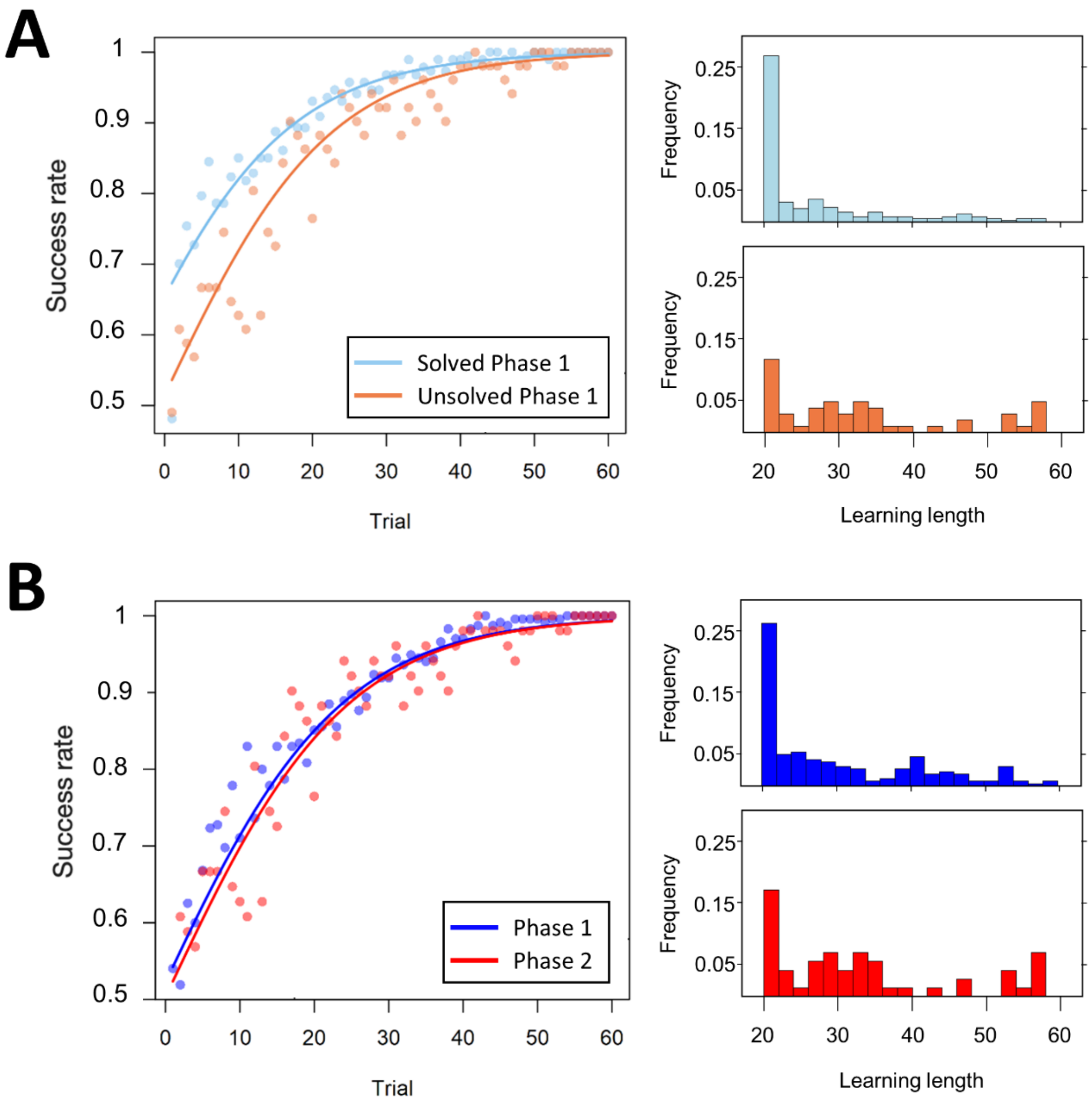

Figure 26. Transfer learning from phase 1 to phase 2 in children. A Curves represent population learning performance for phase 2. Children that solved phase 1 performed better in phase 2 than children who didn't (p= 2e-4, N = 201 vs 56), regardless of age and gender. **B** Blue curve represent phase 1 for children who solved it. Red curve represent phase 2 for children who didn't solve phase 1. This comparison was meant to act as a proxy of phase 2 performace with no prior training. No significant differences were found (p = 0.75, N = 252 vs 56).

4.2. Mathematical modelling of time compaction effect on behaviour

The reported experimental results reveal that a time compaction based mechanism is involved in human decision-making. To shed light into how this mechanism works, a probabilistic model that describes the participant's behaviour during the experiment was developed. Since men were more prone to exploit time compaction, the model will be compared to their results.

The model simulates the process of finding hidden rule 2 (phase 2). The probability of a successful answer at each trial is quantified based on the following assumptions:

- Due to the two-choice nature of the task, both positive and negative feedbacks are informative, so the association stimulus-key is learned after the first stimulus presentation (if the pressed key is not correct, then the opposite one is). Thus, wrong answers to repetitions of the stimulus are due to faulty recall.
- The probability of a correct recall exponentially decays with the trial, i.e., the forgetting rate. The decay rate does not depend on the specific stimulus but on the number of times a given stimulus has appeared.

Thus, the model estimates the probability *P* of a successful answer of a participant at each trial *T* in phase 2 of the experiment. Such probability can be expressed as

$$P_G(T) = 1 - \gamma_G(T)\delta^T,$$

where δ is the decay exponent and $\gamma_G(T)$ is the decay rate that depends on the trial and on phase 1 of group *G*. As time compaction biases Favoured and Hampered groups relative to the Control one, favourably conditioned participants start phase 2 with a set of associations already learned, whereas hampered participants need to re-elaborate the hidden rule. Therefore, for the different experimental groups, the decay rates follow this relationship: $\gamma_F < \gamma_C < \gamma_H$, whose parameters were fitted to the experimental data.

Besides, in experiments, average success probabilities of 0.97 and 0.88 were observed for men in Favoured and Hampered groups, respectively, and 0.91 considering together women and Control men. Thus, an additional data-driven assumption was introduced in the model:

- If a stimulus is repeated four or more times, then the recall probability reaches 1, and hence the pressed key will always be correct.

Time compaction is considered through the associations between situations and keys to be learned during phase 2, after previous exposition to phase 1. It can be assumed that the Favoured group learns associations for two DM situations in phase 1, so the remaining four non-DMs have to be learned in phase 2. In contrast, the Hampered group must re-elaborate the two associations made for DMs in phase 1, since those lead to wrong answers in phase 2.

The model describes the probability of a successful answer at each trial T for the Favoured, Control, and Hampered groups by:

$$P_F(T) = 1 - \frac{1}{3}\left(\frac{5}{6}\right)^{T-1}[1 + \alpha(a,T) + \beta(b,T)],$$

$$P_C(T) = 1 - \frac{1}{2}\left(\frac{5}{6}\right)^{T-1}[1 + \alpha(a,T) + \beta(b,T)],$$

$$P_H(T) = 1 - \frac{1}{2}\left(\frac{5}{6}\right)^{T-1}\left[\frac{4}{3} + \alpha(a,T) + \beta(b,T)\right],$$

where α and β stand for the recalling terms for the second and third appearances of a stimulus, respectively, and *a* and *b* denote the corresponding recalling rates. Fitted values for the Favoured, Control, and Hampered groups were: (*a*,*b*) = (0.1797, 0), (0.2194, 0.0549), and (0.0832, 1.2166), respectively.

These equations were then used to simulate the learning process during phase 2. To this purpose, a set of virtual participants ‘‘responding” to the same input sequences used with human subjects was created. Briefly, every simulated participant was engaged in a Monte-Carlo procedure and its answers were deemed correct whenever the recalling probabilities surpassed a given threshold. The process is iteratively repeated until the participant reaches the same learning criteria set in the actual experiment (18 successes in the last 20 trials). A comparison of experimental results against simulations shows there is remarkable agreement between real learning data and theoretical predictions for Favoured and Control groups (Fig. 27). Therefore, the model, built on top of mechanisms that might be playing a role in the participants' behaviour, provides additional support for time compaction.

Nonetheless, there is a deviation between the theoretically predicted distribution of individual learning lengths and experimental data for Hampered group, which means that the model does not capture accurately the particularities of this group's behaviour. For example, the learning of

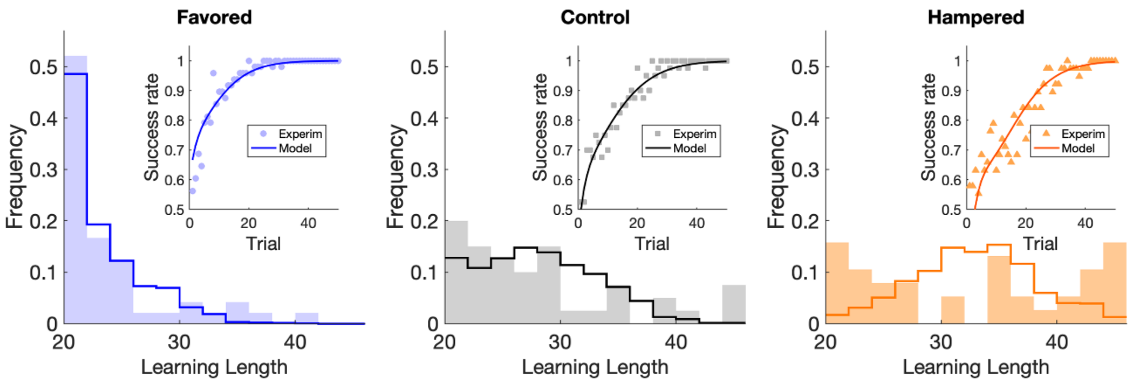

Figure 27. Probabilistic modeling of time compaction. Main panels depict individual learning performance. Histograms correspond to experimental data and stair-like curves correspond to simulated data. Insets depict the population learning process. Dots correspond to experimental data, whereas curves show the model predictions, i.e., the successful answer probabilities $P(T,\gamma)$. Data from Villacorta-Atienza et al. (2021).

hampered participants could require more than two stimulus appearances, while the model is based on two parameters only. However, a more likely reason is the influence of exogenous factors not included in the model, such as motivation, frustration or tiredness.

4.3. Time compaction in a biological neural network

Considering that time compaction might be a universal mechanism potentially exploited by organisms with basic nervous systems, here it is explored whether a neural model comprising a minimal set of biological assumptions is able to exhibit functional properties compatible with time compaction. The model is inspired by two-choice forced tasks used as proxies of aversive learning in animals (Zhang et al., 2005; Zhang et al., 2007), which explains the decision making process as a result of a feedback-modulated competition between two nodes that integrate perceptual information (Wei & Bu, 2017). The proposed model operates on top of functional phenomena extensively studied in mammals' brain, namely the preplay activity, theta rhythm and phase precession. A brief description of them is provided bellow in order to facilitate the comprehension of the biology behind the model.

Preplay activity refers to the capability of reproducing the trajectory of a moving object in a smaller timescale just from its initial positions, even as early as in V1 visual area (Ekman et al., 2017). Theta rhythm is an oscillatory pattern arising at the neural population level that plays a fundamental role in the processing of visuo-spatial information in the mammalian hippocampus (O'Keefe & Recce, 1993). The low frequency of theta rhythm - below 5 Hz in humans (Jacobs, 2013) - imposes phases of excitation-inhibition that naturally arranges neural activation within time intervals or windows, forming discrete codification units. Hippocampal neurons in the same window respond only to stimuli found in certain regions, forming what are known as receptive fields (RF), which in this context would correspond to the region of space that a cluster of place or spatial view cells is sensitive to when it is occupied by an object. These receptive fields follow a Gaussian-like distribution, so that the further the object is from its centre the weaker the response it evokes in the cell. However, it's been shown that place cells' RFs become highly asymmetric with experience, likely due to synaptic plasticity phenomena (Mehta et al, 2000). The interplay between the theta rhythm and the RFs gives rise to the phenomena of phase precession, that allows the compaction of the space-time information of a moving object (O'Keefe & Recce, 1993). This is achieved by reproducing ordered sequences of place cells' activation patterns, which are compressed within excitatory phases of theta rhythm with respect to its behavioural counterpart and anticipates actions in the near future (from miliseconds to seconds).

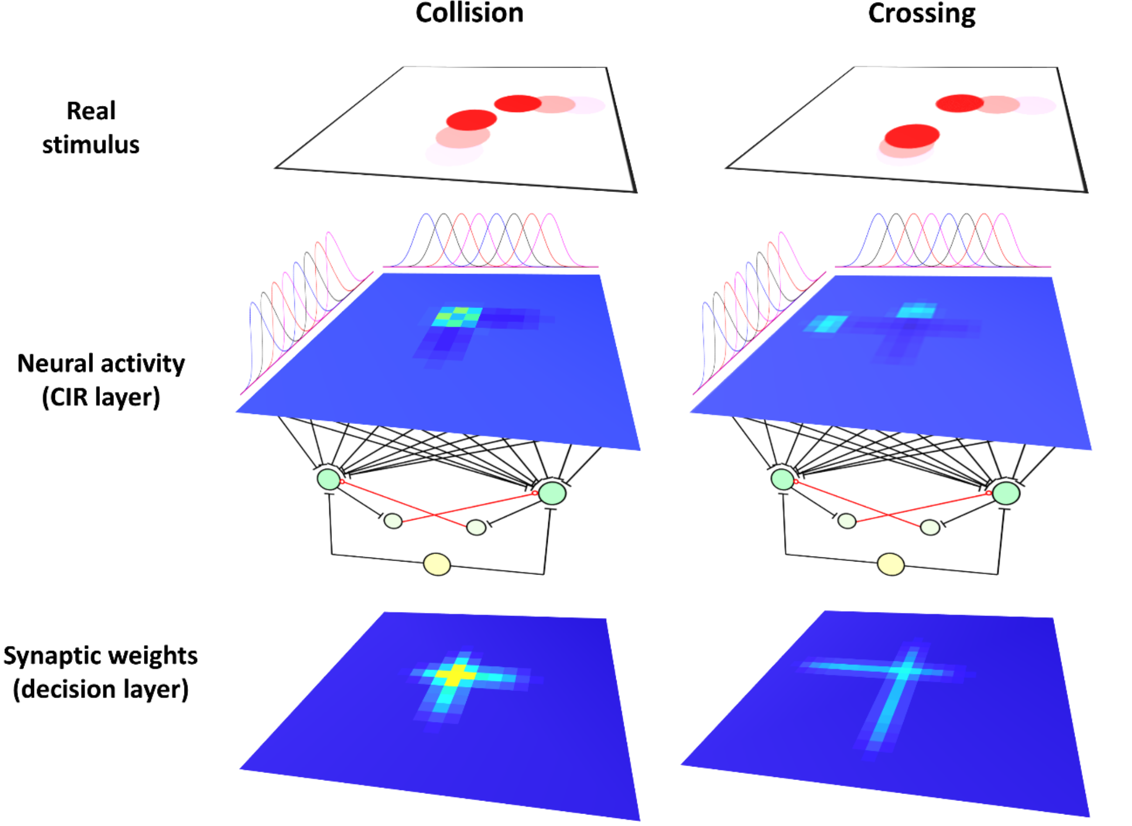

Figure 28. Bidimensional schema of the neural network. Collision and crossing stimuli are coded as sequential activation of CIR neurons' receptive fields. Note that neural activity in CIR layer corresponds to predictions in internal space, not to the actual perceptual experience (i.e. circles in real stimulus have not collided/crossed paths yet, whereas in CIR layer interactions are already represented). After training, synapses connecting each CIR neuron to the active decision neuron are weighted according to the reinforcement or depression process mediated by STDP, leading to the matrices shown at the bottom. Brighter colours correspond to higher synaptic weights, and the maximum value can be found in neurons coding the interaction event (i.e. collision).

Thus, the model presented here consists of a neural network with a three-layer structure, from top to bottom: perceptual or CIR layer, decision layer and feedback layer (Fig. 28). CIR layer is a 2D matrix functionally equivalent to a set of overlapping receptive fields (RFs). This bidimensional matrix is used to represent dynamic stimuli that involves collision and crossing trajectories. Note that this representation is of predictive nature, so collision should be understood as coincidence in mental space, not physical contact in the real world. This is achieved by combining the aforementioned preplay and phase precession principles, which allows to mentally reconstruct patterns and trajectories just from the stimuli's initial positions.

Decision and feedback layers are at the core of the network's functionality. Following a given stimulus, neurons in the decision layer compete to be the one that sends its output downstream, so that it can receive feedback on whether or not the right decision was made. The decision neuron with the highest firing rate gets to communicate with the feedback layer, while inhibiting the contrary via reciprocal interneurons. Thus, one decision neuron activates whereas the other remains silent. This is important because only synapse weights belonging to the active decision neuron are modified. Weights represent the synaptic strength between a neuron in CIR layer and decision neurons, and are modulated as positive reinforcement following success; otherwise, weights are penalized. This modulation is achieved by means of an STDP mechanism, so that the concurrence of a feedback presynaptic spike and a preplay postsynaptic spike within a time window gets to alter the weights between neurons in the CIR layer and the active decision neuron. Weights corresponding to the silent decision neuron are not modified but undergo exponential decay due to inactivity.

Therefore, the objective of the network is to correctly classify stimuli with collision trajectories and stimuli with crossing trajectories, in a trial-and-error fashion. To assess the extent to which time compaction principles arise from such a simple network, a set of virtual experiments was performed. Variables used to quantify the network's performance after learning include: (1) maximum synaptic weight between CIR layer and active decision neuron, as an estimator of memorization; (2) inter-spike interval, as the elapsed time between consecutive spike events; and (3) firing rate, as spikes per seconds. These experiments exploit the network's functionalities and are exposed below from basic classification to more complex generalization tasks, alongside the rationale that explains how exhibited behaviours might be compatible with time compaction assumptions.

Interactions are horizons of prediction

In a first approach, the network was fed with dynamic stimuli moving either in collision or crossing trajectories. Within a single learning session, only one type of stimuli was shown, so no direct competition between them took place. After the learning phase, the highest synaptic weights matched with prediction windows in the vicinity of the collision event (70 ms) (Fig. 29A). For crossing trajectories, max weight decreased for positions farther from the collision coordinates (offsets). Following the weight reinforcement at CIR nodes corresponding to the collision area, the inter-spike interval of the active decision neuron reaches a global minimum right after the collision event (40 ms) (Fig. 29B). Examining the matrix of synaptic weights, maximum activation occurs after a prediction window of 70 ms, right after the mental collision takes place (Fig. 29C). This is coherent with time compaction hypothesis, by which interactions are important because they are horizons for prediction, so anything that happens afterwards is affected by a greater degree of uncertainty that grows as the prediction moves beyond the last interaction (i.e. collisions).

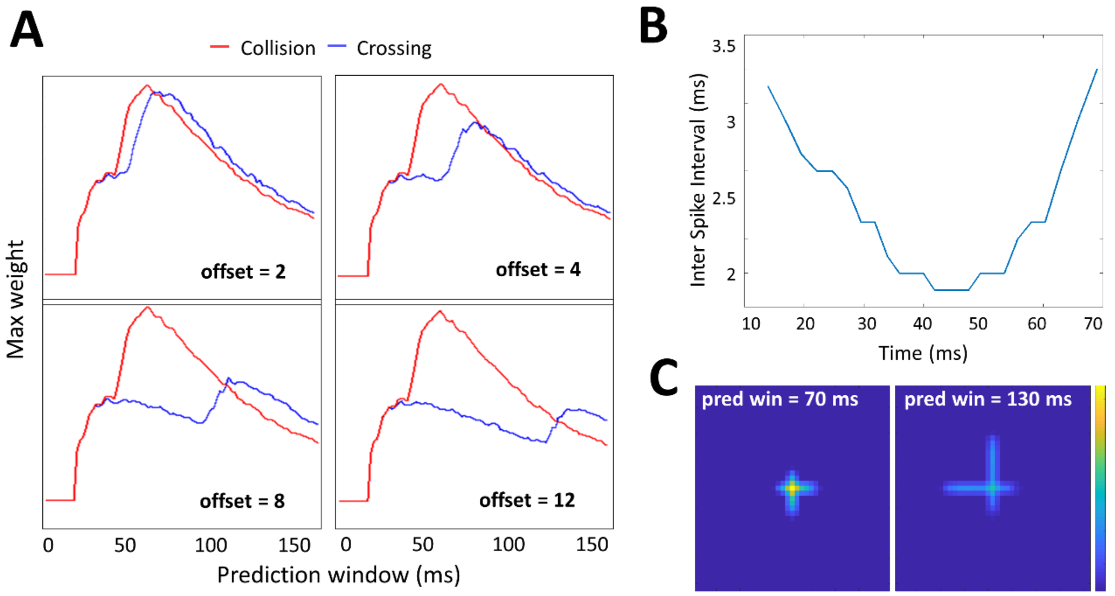

Figure 29. Learning performance after a training session. Plots correspond to measurements taken for the active decision neuron. **A** Maximum synaptic weights of crossing stimuli gradually decrease as the stimuli's offset increases. The bimodality corresponds to the consecutive passage of the crossing circles through the same central spot at different times. Offset refers to the distance that crossing stimuli appear from the predicted interaction point, so an offset = 0 would be identifical to an actual collision. Prediction window represents the amount of time that mental prediction is allowed to develop, starting from the last known position of the circles in the real world. **B** Frequency of spiking events rises right after the prediction of the collision event takes place, at 40 ms, which translates into a minimum in the inter-spike interval. **C** Synaptic weights of collision stimuli consistently surpass those of crossing stimuli after aligning the optimal prediction windows (max weights in A). Colorbar represents weight value (dark blue for lowest and bright yellow for highest).

Interactions are salient events in memory

Starting from the network already trained to recognize collisions shown in Figure 29, the CIR layer is fed with low intensity inputs, which serve as a proxy for scenarios of sparse attention or poor quality environmental information. If collisions were not internally coded as salient events, an observer paying little attention to a dynamic situation might not represent at all the collisions taking place, putting itself in potentially dangerous circumstances. As evidenced in Fig. 30A, the active decision neuron elicits an increase in its firing rate following a collision input with intensity of roughly one order of magnitude below the inputs used for training. The neuron had the same response even with new trajectories that it hadn't seen before but shared the already known collision point (Fig. 30B). Moreover, in both cases, the neuron starts firing only when the prediction of collision takes place. This replicates one of the most crucial hypothesis of time compaction, that future interactions in dynamic environments are coded in memory as salient events, which facilitates its retrieval and allows for generalization to new situations.

To further illustrate this functionality in more sophisticated environments, the network was trained with situations comprising multiple dynamic stimuli (Fig. 31). During later recalling, the network was confronted with distracting stimuli, closely resembling the ones it has been trained on. This was done for different kinds of stimuli consisting of collisions, crossings and no interactions (control environment with parallel trajectories), shown to the network one at a time. The network was able to correctly distinguish the memorized stimuli from the distractors in all scenarios, and it is noteworthy that the firing rates of the active decision neuron for collisions almost doubled the firing rate for the control stimuli (Fig. 31, right column). This result emphasizes how interactions act as organizers of attention and hotspots of information, providing robustness to the internal representation of dynamic situations.

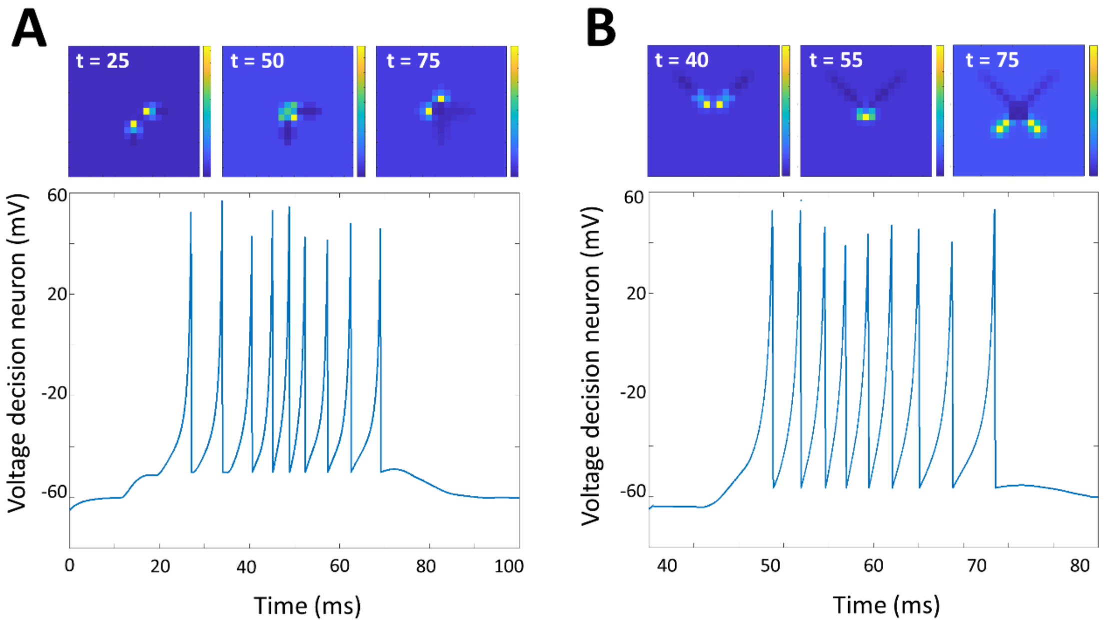

Figure 30. Spiking activity in a generalization task. Plots correspond to the active decision neuron of a network pre-trained with collision stimuli, as in Fig. 29. **A** Feeding the network with low intensity collision stimuli elicits spiking behaviour in the active decision neuron. Current intensity was 1/10 of the intensity used for training the network. Top panels depict the sequence of predicted positions in CIR layer that reached the decision neuron at 25, 50 and 75 ms. **B** Decision neuron is able to recognize collision stimuli with trajectories that it has never been exposed to before. Top panels depict the sequence of predicted positions in CIR layer that reaches the decision neuron at 40, 55 and 75 ms. Colorbars represents receptive field’s activation levels (dark blue for lowest and bright yellow for highest).

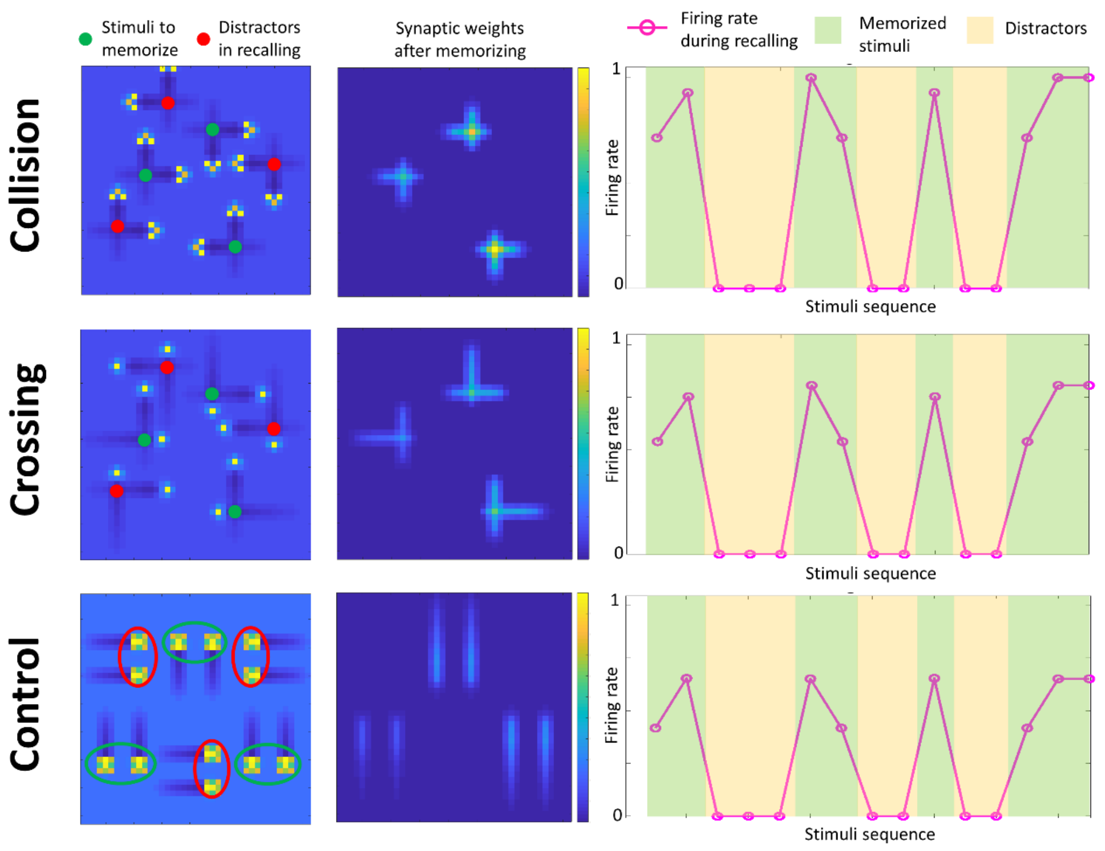

Figure 31. Recalling performance in noisy environments. First column corresponds to stimuli's predictions at CIR layer. Second column corresponds to synaptic weights between CIR layer and the active decision neuron after a training session. Third column corresponds to the firing rate of the active decision neuron after being exposed to a sequence comprising memorized and unknown stimuli (distractors). Top, middle and bottom rows correspond to stimuli with collision, crossing or parallel trajectories. Note that stimuli are fed to the network one at a time, although the matrices shown here depict the full set of stimuli provided to the network. Firing rate is normalized to facilitate comparison between types of stimuli.

Interactions accelerates learning in dynamic situations

Here it is explored whether any differences can be found between the learning rates of collision and crossing stimuli. To this purpose, the network is exposed to two types of stimuli (Fig. 32A, stimuli), a control one consisting of two circles moving in parallel trajectories, and another one comprising two circles that collide in the central spot. The network is fed with both stimuli in successive trials during the learning phase, so actual competition takes place between the decision neurons to ensure that the correct one is active after the apparition of the corresponding stimuli. A direct comparison between their firing rates reveals that the activity of the decision neuron sensible to collisions at trial 7 is comparable with the activity of the decision neuron specific to control stimuli at trial 10 (Fig. 32A, bottom plot). In other words, for a given number of trials during the learning phase, the decision neuron that detects collisions is more active than its counterpart. This is also reflected in the matrix of synaptic weights (Fig. 32A, weights) and in the maximum weight achieved throughout multiple prediction windows, which is halved for control stimuli in contrast to collisions (Fig. 32B). In essence, these results support the idea that internal representations of dynamic situations are learnt faster and with less effort when interactions among its elements are involved. This is a direct consequence of time compaction, as the elements in the environment that will interact in the future are represented solely by such interactions (many-to-one relationship, less information to learn), whereas elements that will not interact are still represented by themselves (many-to-many, more information to learn).

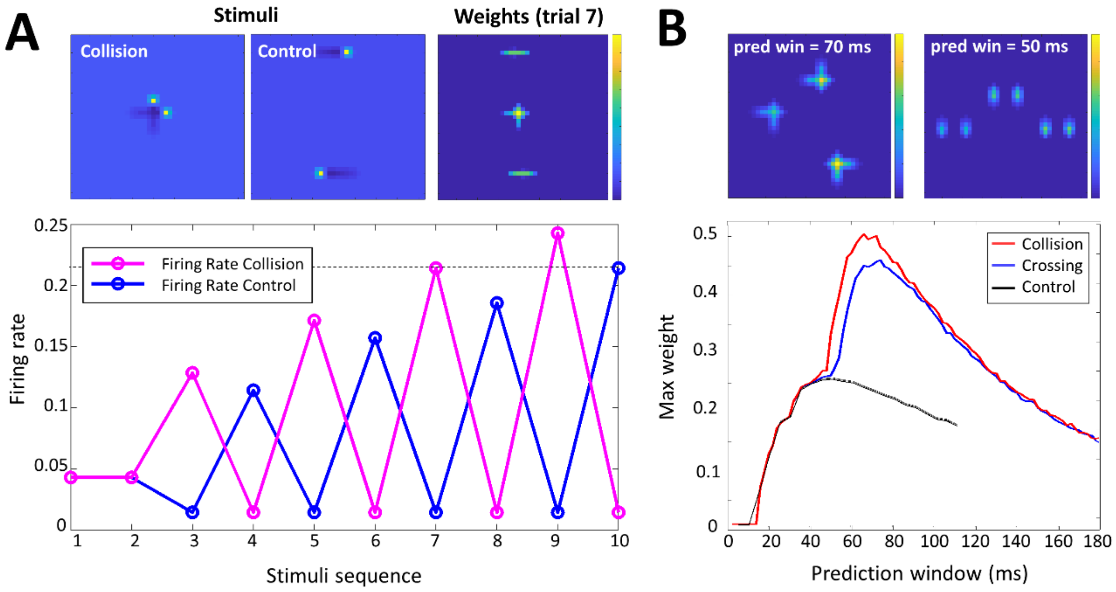

Figure 32. Learning performance in a competition task. A Top panels depict stimuli's predictions at CIR layer and the matrix of synaptic weights after learning. Both decision neurons are represented simultaneously in the weights' matrix for sake of clarity. Bottom plot represent the firing rate of the decision neuron that wins each trial, so from trial 3 and on the network never fails, as the active neuron is always the correct one. Horizontal dashed line emphasizes the fact that firing rates elicited by collisions reach a certain level of activation prior to control stimuli. **B** Maximum synaptic weight for control stimuli peaks at 50 ms and its value halves that of collision stimuli. Top panels depict matrices of synaptic weights for the optimal prediction windows of collision (left) and control stimuli (right).

5. DISCUSSION

Questions addressed in this work stem from the multiplicity of strategies that animals develop to survive in their natural environments. From the pool of potential behaviours that might be feasible in a particular context, spatial and temporal features of the real world act by funnelling down the ones that optimize survival chances. How does the brain coordinate the computation of such behaviours? Are there any functional mechanisms capable of managing the stream of spatiotemporal information? Here we report the first experimental evidence that time compaction does exist as a functional mechanism of human cognition, which provides a robust framework for dealing with such questions.

Primary defensive and evasion behaviours have been found to be encoded mainly by temporal features of the environment, such as time-to-collision coding of threatening looming objects (Wang & Frost, 1992; Yilmaz & Meister, 2013). In simple but non-trivial situations, such as interception of virtual balls under variable gravity conditions, spatial prediction has been shown to override temporal information (Russo et al., 2017). Nonetheless, more often than not, both dimensions are cooperatively coded in the brain, as revealed by shared neural bases operating both predation and prey behaviours (Evans et al., 2019). Not only are these evidences tuned with the theory of time compaction, but are also in its foundational basis.

In the time compaction framework, the connection between mental abstraction of static and dynamic situations arises from the hypothesized similarity between their internal representations. The experimental setup in the present work was particularly designed to exploit such similarity, by causing interference between representations and associations stored in memory. If time compaction held true, modulation of the learning process should be predictable from the level of agreement in association rules and internal representations of static and dynamic stimuli, in consecutive phases.

From the results described in this manuscript, it can be stated that time compaction is a functional strategy oriented towards the comprehension of dynamic environments, even when the subject is neither explicitly interested in interacting with its surroundings nor directly involved in such interactions. Conversely, time compaction may be acting as a vector for knowledge acquisition through observation, since skills critical for surviving can be internally experienced without being exposed to potentially dangerous situations (Frank et al., 2013). Although the running hypothesis is that this basic mechanism might be present in animals with some degree of cephalization, the human brain constitutes the premier testbed, as it is particularly capable at handling mental descriptions of external objects that allow predictions of future events (Ramos, 2014). This process is mediated by manipulation of internal states that represents objects alongside the rules governing their behaviour.

5.1. Alternative explanations

To validate time compaction as the most plausible mechanism behind the observed data, alternative interpretations that could be compatible with the experimental findings are discussed here. A short summary is presented at the end of the section for clarity purposes.

First, dynamic and static stimuli show no unpredicted spatial compatibility. The experimental differences between learning performance for compacted and non-compacted dynamic stimuli are in line with time compaction *a priori* assumptions. However, as the focus is put on the relationship between SM and DM stimuli to explain the results, there might be shared features between non-SM and non-DM stimuli that could also explain the learning differences. Since the final position of the red circles displayed in the screen is different for each of the six dynamic stimuli and it is a spatial information, it could be possible that some sort of spatial compatibility exists between such a final position and the static position of the red circle in the static stimuli. A rationale for discarding this option is provided below.

An initial consideration would be that Favoured and Control groups differ uniquely by a single static stimulus: the SM stimulus for Favoured group and a third non-SM stimulus for Control group. As a result, any unexpected spatial compatibilities between non-DMs and non-SMs stimuli should be equal in both groups. Therefore, its effect cannot explain the learning differences. Second, the dynamic stimuli's spatial information only differs in the final positions of the red circle, while the initial positions and all the trajectories remain the same. Then, by assuming a link between the final positions of the red circle in dynamic stimuli and its locations in static stimuli exists, the resulting learning process would be inconsistent with the experimental results.

This issue is summarized in Figure 33, which shows the static and dynamic stimuli with their respective key assignations organized in tables. First and second rows contain the dynamic and static stimuli with the assigned keys. The stimuli in each column are arranged such that they

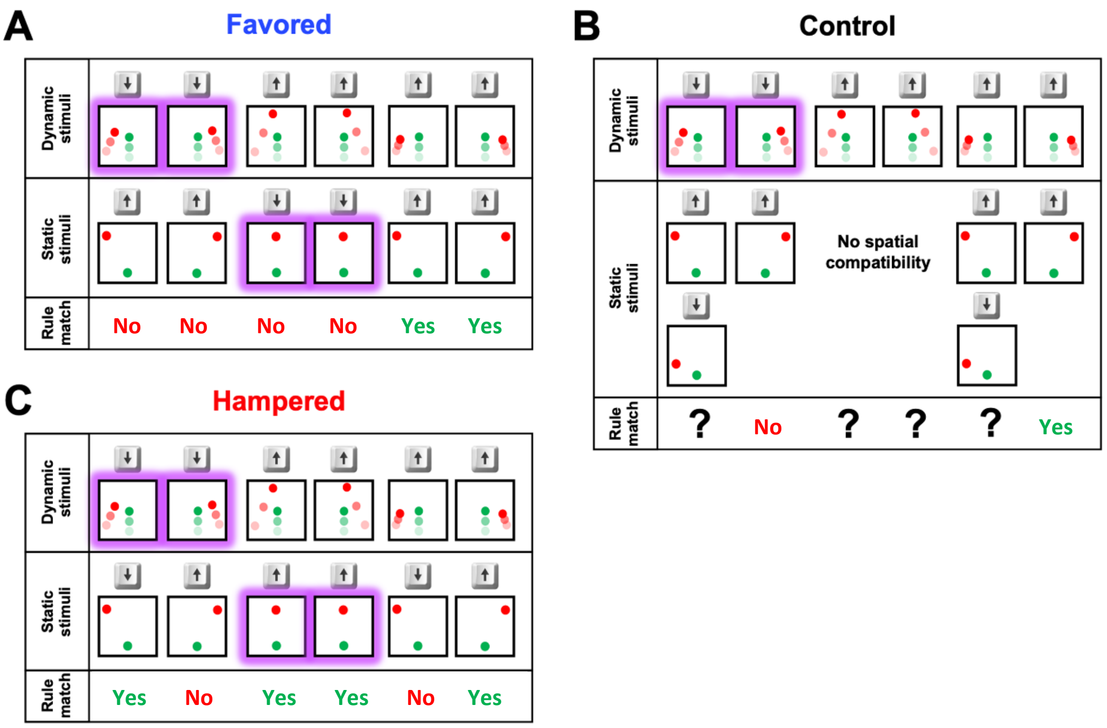

Figure 33. Potential spatial compatibility effects due to the displayed final position of the red circle. Comparison between phase 1 and phase 2 stimuli-key associations. Compatible stimuli are highlighted in purple. **A** Favored, **B** Control, and **C** Hampered groups would show different learning processes than those described in this work, if the displayed final position of the red circle in the dynamic stimuli and the position of the red circle in the static stimuli would have been used to figure out the hidden rule 2. In particular, both Favored and Hampered participants would have a stable pattern transferred from phase 1 to phase 2, whereas for Control participants there would be four dynamic stimuli with no clear correspondence with the static stimuli. This should induce a higher dispersion of data for this group than for the former ones, something not observed in the experimental data.

have the final position (for dynamic stimulus) and the static position (for static stimulus) of the red circle at the same lateral position (left, centre, or right). To check whether this spatial compatibility has some impact over the learning of the hidden rule 2, the assigned keys are compared. If they match/mismatch, a "Yes/No" label is included in the corresponding column of the third row, meaning that, in case of existing such a transference of spatial information between static and dynamic stimuli, it would facilitate/hamper the discovering of the hidden rule 2. Besides, if the final positions play a role, it should be reflected in the rules written by the participants after the experiment. However, the participants answered in terms of collision or velocities and did not refer to the final positions.

An additional concern may be a possible transfer of spatial information not explicitly displayed in the stimuli, such as the hypothesized relationship between the locations of the red circle in static stimuli with the predicted final positions in dynamic stimuli. When circles in non-DM stimuli disappear, participants mentally carry on and complete the movement in multiple ways, and thus the extracted ‘‘final” positions change from subject to subject. This renders the transfer of a stable rule relating non-SM to non-DM stimuli unlikely. Such variability in the mental pattern completion is not an issue for DM stimuli, given that time compaction sets collision as a natural mental boundary. Actually, Figure 33 shows that the consequences of this spatial compatibility is the opposite to the reported results: during phase 2, the Favoured participants should learn slower than Hampered subjects, whereas the participants of the Control group should exhibit higher dispersion of data due to the variability in their answers, since there is no stable pattern transferred from phase 1 to phase 2.

The possibility that dynamic stimuli might contain implicit bias was also examined. Circles' positions in the screen's laterals and movement directions could potentially induce a preference for some stimuli over the others (Maass et al., 2014). To prevent this, setup was designed using symmetries that avoids the bias of the DMs over non-DM stimuli. Red and green circles move with different velocities and along different trajectories (neither parallel nor opposite). This discards the possibility that some stimuli could have been differently processed internally than others (Murray, 1995). Also, feedback provided during learning in the form of a tick or a cross does not transfer any additional visual information that could be artificially linking SM and DMs.

The behavioural task proposed in this work was intended to modulate the learning process by causing interferences in associative memory (Kiyonaga & Egner, 2014). One may argue that learning should not occur at all in the facilitated dynamic scenario, given that the arrow-CIR association has been already learnt for the static case, so participants in Facilitated group should start phase 2 with 100% accuracy, with no room for further improvement. Two balancing factors were introduced in the experimental design to avoid this issue. First thing to point out is that collision was never explicitly displayed on screen, meaning it only occurred in the participant's predictive mental space. There are no visual cues for the salient event position shared between the dynamic and static stimuli; for that reason, CIR matching between dynamic and static ought to happen without turning to replay in visual pathways. The second balancing strategy involved the inclusion of dynamic stimuli whose internal representation never matched with the static CIR, (i.e., circles in crossing in lieu of colliding trajectories), which would create unforeseen scenarios for the subjects and induce a forget effect when randomly intercalated throughout the stimuli sequence presentation. There is then a certain level of noise in the learning process of the dynamic stimuli, either it be basal due to differences in the predictive capacity of each participant or modulated by random presentations of non-matching CIR scenarios, that prevents transfer of perfect learning between the two phases of the task.

Summarizing, alternative explanations here discarded include: (i) spatial compatibility between non-SM and non-DM stimuli, which should bias the learning process in a way that contradicts the experimental results; (ii) stimulus-response compatibility effect in phase 2, which was counterbalanced by randomizing the key assignment to symmetric pairs of stimuli; and (iii) transfer of information from predictions, which should result in high variances not present in data from control groups.

5.2. Gender differences

Although time compaction was conceived initially as an elementary gender-independent cognitive mechanism, its salience in the proposed experiments was statistically significant in men but not in women. Nonetheless, it is remarkable that women's learning performance was comparable to that of men control group. Moreover, strategies verbalized by women in accordance with time compaction (responses referring to collisions) were independent of the learning length, whereas men's strategies compatible with time compaction were heavily biased towards fast learners. Thus, the data supports the idea that women also exploit time compaction, probably alongside other decision-making strategies, which might have hindered its saliency.

For that reason, more complex mechanisms beyond spatial perception should be taken into consideration. These might include (1) mental management of spatial visualization information criteria for establishing the stimulus-key relationship (when a key must be pressed after visual information disappears) and (2) mental reproduction of the animation in subjects who verbalized the rule in terms of 'collision'. Regarding (1), it has been described that there are no significant differences between men and women when performing simple spatial visualization tasks (Burin et al., 2000; Voyer et al.,1995), although men tend to outperform women in virtual navigation of complex environments (De Castell et al., 2019). Regarding (2), rule learning is strongly influenced by spatial memory, since participants must recall the stimulus-key associations previously memorized to correctly answer after each stimulus presentation. Given the dynamic nature of the stimuli and the simplicity of circles' trajectories, a coding shortcut alternative to time compaction could be simple based on the circles' initial and final positions. Such a processing requires spatial memory of the object location, which has been found to pose gender bias in favour of women (Voyer et al., 2007). Circles have also been described to favour women's performance during object location memory tasks (Voyer et al., 2007). In consequence, among the several cognitive mechanisms involved in the processing of dynamic stimuli akin to the ones used in this work, gender bias is absent or favourable to women, at best.

Gender differences reported here are in consonance with studies exploring the cultural impact of sex-role divisions in early human societies. It’s been shown that men follow holistic strategies to collect information regarding spatial relations among elements in the environment (Peña et al., 2008). On the contrary, women are more prone to segmentary approaches that put a special focus on relevant features of the elements instead of their relationships (Picucci et al., 2011). As a consequence, men tend to outperform women in mental manipulation of objects (image rotation, transformation, projection, etc.), which might be interpreted as an essential skill during agonistic behaviours such as throwing objects and anticipating preys’ trajectories in hunting encounters (Kolakowski & Malina, 1974; Lawton & Hatcher, 2005). Likewise, women’s better performance in object's location memory tasks would be compatible with foraging roles, which could have benefited from good memorization of the whereabouts of food sources (Ecuyer-Dab & Robert, 2007; New et al., 2007). Thus, sex differences supported by the hunter-gatherer hypothesis’ literature (Silverman et al., 2007) are coherent with the findings of the present work. Whereas men preferably participated in situations that required optimizing fast and real time interactions within dynamic situations (e.g. hunting, chasing or fighting), the presumed role of women as gatherers would be in line with abilities (e.g. searching, collecting or fine manual handling) that would not recruit time compaction over other cognitive strategies; though, as discussed, time compaction also belongs to women’s cognitive repertoire.

5.3. Age onset

Not unlike other cognitive traits, results in this work regarding children show that time compaction is dependent on the stage of maturation. It’s usually accepted that concrete thinking is developed during childhood focusing first on physical things and then on abstract elements (Inhelder & Piaget, 1953). Presumably, all children involved in the present study should have been capable of internally representing the dynamic stimuli they were exposed to, considering that mental imagery regarding movement emerges in the interval between 7 to 8 years old (Marmor, 1975). Moreover, it’s been described that the ability to perform mental simulations of events, objects or scenes in the absence of perceptual input reaches its maximum in adolescence and declines with ageing (Cornoldi & Vecchi, 2004; Dror & Kosslyn, 1994). In this sense, previous evidence suggests that body-related stimuli facilitate children’s performance in mental transformation tasks (i.e. it is easier for children to imagine the rotation of a hand rather than rotation of a cube) (Iachini et al., 2019; Jacewicz and Hartley, 1979). This is supported by studies showing that in children, poor coupling between perception and action in dynamic collision avoidance tasks can be reversed considering body anthropometrics as a performance measurement (Rapos et al., 2019). However, in the experiments conducted in the present work, it was found that children that solved either phase 1 (static stimuli) or phase 2 (dynamic stimuli) as their first phase, performed equally. Additionally, no significant gender differences were found, as opposed to literature regarding sex-biased performance in static spatial tasks (i.e. mental transformations), typically found in children (Kerns and Berenbaum, 1991; Levine et al., 1999).

These findings point to the existence of an immature form of time compaction that could be acting as a baseline cognitive mechanism during childhood, not salient enough to overtake other strategies yet. This is coherent with the lack of preference for time compaction reported here in children, which might be indicative of an internal representation system that depends more heavily on embodiment than pure abstractions during early stages of human growth.

5.4. Probabilistic model of experimental behaviour

Experienced situations can be represented and stored in memory as static maps or CIRs, containing the information needed to deal with them. CIR management allows for efficient processing workflows that include learning, storing, comparing, and structuring of experiences (Villacorta-Atienza & Makarov, 2013). Then, when the subject faces real-time complex scenarios, the corresponding CIR can be quickly recalled from memory to generate fast and accurate responses in narrow time windows. Moreover, time compaction-based cognitive architectures provide an operational mechanism for the synergistic coexistence of so-called model-based (MB) and model-free (MF) computational approaches (Lee et al., 2014).

MB computation typically reflects prospective recreation of potential outcomes and future actions, which would correspond to a ‘conscious’ process of CIR construction. On the contrary, MF starts from experiences learnt *a priori*, which makes it faster and consistent with CIR recalling capabilities to generate effective and rapid ‘subconscious’ responses. Following the event coding paradigm (Hommel, 2019), these responses are structured not only as sequences of actions, but also involve semantic content, i.e., the meaning of such actions in the global context of the task. The latter is a compulsory requirement to generate sophisticated strategies that adequately chain movements and behaviours. Then, the semantics to each potential response are encapsulated within action-based internal representations supported by time compaction (Calvo et al., 2020).

Therefore, generation of memories plays a pivotal role in the time compaction paradigm. This has been explored here theoretically, through a probabilistic model that aimed to simulate the learning process of the human subjects involved in the experiment. The model was able to replicate the behaviour of real participants by incorporating three common assumptions of any process of memory and retrieval (Rubbin & Wenzel, 1996; Wixted, 2004): (1) heterogeneity of forgetting rates, in this case corresponding to different experimental groups, (2) consolidation of memory traces over time, so learning occurs by trial and error, and (3) competition between memory traces, incorporated in the model by an exponential decay rate dependent on the number of trials between successive repetitions of a given stimulus. The latter was based on the widely accepted notion that the decline in memory performance with time or intervening events can be characterized mathematically by the families of power and exponential functions (Wixted & Ebbesen, 1991). Simulations have supported this analytical description of forgetting, which has been shown to adjust well to the empirical data.

For that reason, in this work the highlight was put on how forgetting was affected by experimental manipulations. One drawback of the model is that it didn’t fully capture the individual learning performance of the Hampered group, probably due to external factors not included in the model. It has been postulated that successfully triggering behaviour in humans is heavily related to the ability and motivation involved in a particular task (Butzin, 1971). Thus, as Hampered participants needed more trials to finish the experiment and, according to time compaction, had to forget and re-learn the hidden association rule in phase 2, one possible explanation is the loss of motivation due to tiredness or the perception that their ability didn’t match the new requirements of the task. Nonetheless, Favoured and Control groups performance was successfully replicated both at the population and individual levels, which informs that fundamental principles of learning and retrieval could be playing a role as mechanism deeply interwoven with time compaction.

5.5. Neural network model of time compaction

The proposed experimental design and the results described so far suggest that CIRs of dynamic situations operate at the cognitive level, beyond early visual pathways (Delle Monache et al., 2017; Russo et al., 2017). In this sense, time compaction expands the concept of cognitive maps (Epstein et al., 2017), providing a functional generalization to the internal representation of static scenarios. Hippocampus is at the core of the generation of cognitive maps during free navigation to unmarked locations, defined by their relationships with the environment (e.g. a spot where reward is likely to occur but has no other identifiable features otherwise). However, it’s been described that cognitive maps are not involved in the navigation towards visible static goals (Morris et al., 1982), whereas the avoidance of visible, dynamic objects does rely on the hippocampal formation (Telensky et al., 2011). This is consistent with time compaction, where time-changing situations are represented by the forecasted relationships and interactions among its elements. From these findings, it seems plausible that neurobiological mechanisms underlying cognitive maps of static scenarios could also play a role in the generation of CIRs in dynamic environments.

Thus, in the present work it was hypothesized that specific cell populations responsible for physical object encoding, such as spatial view cells (Rolls, 1999) and recently characterized object vector cells (Høydal et al., 2019), may also be involved in the encoding of virtual objects, forming the input to the neural network model proposed here. Such a model was implemented with spiking neurons as a neural circuit, and describes the decision-making process as a result of reinforcement learning within a two-choice forced task. This paradigm has been applied in other studies to replicate aversive learning in bees (Wei & Bu, 2017) and more recently to automatize the control of robotic arms based on environmental feedback (Wei et al., 2020).

Dynamic virtual objects were represented within the network as predictive maps of future interactions (i.e. CIRs of collision and crossing stimuli), arising from the deformation of the cell's receptive fields following experience and familiarity with the input event. The predictive nature of the network was based on the combined effect of functional phenomena such as preplay activity and phase precession (Ekman et al., 2017; O'Keefe & Recce, 1993), whereas learning was mediated by synaptic plasticity dependent on timing of spiking events between postsynaptic feedback and presynaptic predictive input (Song et al., 2000). The decision-making step was implemented as a firing competition between two spiking neurons, so ultimately the learning process that took place could be explained as the regulation of receptive fields by synaptic plasticity and feedback. This adjustment was reflected on the connections between the CIR layer and the decision layer, which were controlled by weights indicating the level of activation that reached the decision neurons from the predictive internal representation. As a consequence, the network was able to learn by a trial-and-error procedure, and ended up successfully classifying stimuli consisting of circles with collision and crossing trajectories.

The properties exhibited by the described network were compatible with behaviours expected under the time compaction hypothesis. First, CIR neurons representing predicted interactions (i.e. collisions between elements comprising the stimuli) contained the highest amount of information within their synaptic weights. As a result, the firing rate of the active decision neuron peaked right after collision prediction took place. That was not the case for stimuli with no predicted interactions (i.e. crossings) or for large prediction windows, where synaptic weights decayed below the threshold of spurious uncertainty. Thus, interactions act as boundaries for predictions, serving as the last source of reliable information before the system becomes too unpredictable to adequately guide behaviour.

Second, interactions are organizers of environmental information in memory. When a network pre-trained with collisions was fed with lower intensity stimuli to simulate real situations where sparse or little attention is being paid, the decision neuron still exhibited spiking behaviour in the vicinity of the predicted interaction. This held true even for stimuli with different trajectories never seen before by the network, or in recalling tasks where distractors were interspersed with known stimuli. Moreover, when actual competition between stimuli was introduced in the network, the firing rate and synaptic weights were consistently higher across trials for the decision neuron coding collision stimuli over crossing or parallel ones. This goes in accordance with experimental studies showing that in demanding dynamic tasks comprising moving objects (e.g. cars in a street-crossing situation), subjects avoided collisions more efficiently by taking quick gazes towards non-collision elements (Hardiess & Mallot, 2010), which reflected that collision-prone elements were more likely to be represented in memory rather than fixated by the eye.

The aforementioned procedure of gathering information, creating predictions, generating representations, contrasting with expected outcomes, and correcting them in order to optimize decision-making is compatible with several models of learning and cognitive development (Ramos, 2014). This mechanism of correlated internal representations is also compatible with a Bayesian understanding of cognitive functions (Lee & Wagenmakers, 2014), where incomplete or partial representations still serve as estimators of *a priori* probabilities useful to generate quick yet robust predictions of future events.

6. CONCLUSION

I. Time-changing situations can be internally represented in the human brain as static abstractions. Such compact internal representations, or CIRs, comprise predictions of future interactions, spatially arranged as maps where time is no longer present.

II. There is a preference for men to tackle dynamic situations resorting to time compaction, in contrast to women, who rely on a broader repertoire of strategies.

III. Time compaction is dependent on the stage of maturation, and acts as a baseline yet not salient mechanism at least from nine years of age.

IV. Basic laws of human memory, such as consolidation and competition of memory traces over time, may be involved in the cognitive machinery of time compaction. Mathematical modelling of the experimental results proves to be a powerful tool to gain deeper insight of cognitive phenomena underlying time compaction.

V. Predicted interactions are hotspots of environmental information, serving as mental anchors that structure forgetting and attentional processes. This was supported by a neural network that offered a topography-free implementation of time compaction's principles and a functional paradigm that can be exploited under basic workflows of biological information.

7. FUTURE RESEARCH

The experimental results here reported have confirmed that time compaction is a cognitive policy coupling actions and abstractions. As such, compact internal representations, or CIRs, would be one of the key mechanisms exploited by humans to make fast and reliable decisions in dynamic environments. Future lines of research might delve deeper into the biological soundness of time compaction, by exploring the interplay between time compaction and other cognitive strategies, testing the extent to which sensorial multimodality is involved in the emergence of CIRs, describing the effect of stimuli enriched in semantic content or designing behavioural paradigms that allow investigation in other species. Neuroimaging techniques and electrophysiological recordings may also play an important role to expand the knowledge on the neural substrates involved in time compaction.

Computational approaches have also contributed to expand the potential impact of time compaction. Both behavioural and neuronal models here described operate on the basis that interactions are attractors of attention that are represented in memory as salient events. Future perspectives could include exploring analytical descriptions of recursive cognition, in which two or more cognitive agents are engaged in dynamic, decision-making situations.

Overall, concepts discussed here aimed to offer a generalization of the notion of information, in the sense that all interactions in the real world can be deemed as phenomena of information exchange. According to time compaction, the construction of internal representations can be seen as a special case in which dynamic information is received, comprehended, and modified at the cognitive level, associating features between perceived elements to generate equivalent static predictions. These new internal elements, stripped of any temporal information, are continuously validated by its confrontation with external inputs and by the selection of representations, in relation to its predictive power and its potentiality to improve likelihood of survival. Future research might expand ongoing attempts to implement human-like cognition in automatas, opening the possibility to a seamless integration of robots in daily life tasks.

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Technical Appendix

Statistical summary

Figure	Comparison	Test	Sample size	Statistic	P-value	Code
Fig. 14A	Men Favored v Control	GEE (logit)	48 v 40 (88)	13.1	3e-4	***
Fig. 14A	Men Favored v Hampered	GEE (logit)	48 v 38 (86)	50.9	9.8e-13	***
Fig. 14A	Men Hampered v Control	GEE (logit)	38 v 40 (78)	13.4	2.5e-4	***
Fig. 14A	Women Favored v Control	GEE (logit)	52 v 35 (87)	0.61	0.43	NS
Fig. 14A	Women Favored v Hampered	GEE (logit)	52 v 48 (100)	1.15	0.28	NS
Fig. 14A	Women Hampered v Control	GEE (logit)	48 v 35 (85)	0.01	0.93	NS
Fig. 14A	Men v Women Control	GEE (logit)	40 v 135 (175)	1.44	0.23	NS
Fig. 14B	Men Favored v Control	Cox	48 v 40 (88)	-3.38	7.2e-4	***
Fig. 14B	Men Favored v Hampered	Cox	48 v 38 (86)	-5.51	3.5e-8	***
Fig. 14B	Men Hampered v Control	Cox	38 v 40 (78)	-2.75	5.8e-3	**
Fig. 14B	Women Favored v Control	Cox	52 v 35 (87)	0.028	0.98	NS
Fig. 14B	Women Favored v Hampered	Cox	52 v 48 (100)	0.42	0.67	NS
Fig. 14B	Women Hampered v Control	Cox	48 v 35 (85)	0.30	0.76	NS
Fig. 14B	Men v Women Control	Cox	40 v 135 (175)	0.06	0.95	NS
Fig. 15B	Men Distance·Trial·Group	GLM (logit)	126	4.34	5e-4	***
Fig. 15B	Men Favored Distance·Trial	GLM (logit)	48	3.84	1e-4	***
Fig. 15B	Men Control Distance·Trial	GLM (logit)	40	-2.19	0.03	**
Fig. 15B	Men Hampered Distance·Trial	GLM (logit)	38	-3.12	1e-3	***
Fig. 15B	Women Distance·Trial·Group	GLM (logit)	135	1.91	0.08	NS
Fig. 15B	Women Favored Distance·Trial	GLM (logit)	52	1.88	0.06	NS
Fig. 15B	Women Control Distance·Trial	GLM (logit)	35	0.61	0.54	NS
Fig. 15B	Women Hampered Distance·Trial	GLM (logit)	48	-0.09	0.92	NS
Fig. 16A	Learning Length·Gender interaction	GLM (logit)	261	-2.003	0.04	*

Figure	Comparison	Test	Sample size	Statistic	P-value	Code
Fig. 16A	P(Men answer in collision terms)	GLM (logit)	126	-3.23	1.2e-3	**
Fig. 16A	P(Women answer in collision terms)	GLM (logit)	135	-0.43	0.67	NS
Fig. 16A	Gender·Conditioning interaction	GEE (id)	261	5.04	0.28	NS
Fig. 16B	Men v Women response time	GEE (id)	126 v 135 (261)	0.72	0.4	NS
Fig. 16C	Response time Favored v Control	GEE (id)	100 v 75 (175)	2.24	0.13	NS
Fig. 16C	Response time Favored v Hampered	GEE (id)	100 v 86 (186)	0.58	0.45	NS
Fig. 16C	Response time Hampered v Favored	GEE (id)	86 v 75 (161)	0.66	0.42	NS
Fig. 17B	Stimulus difficulty and Learning Length	GLM (id)	261	0.92	0.63	NS
Fig. 18	Men Favored v Control	GEE (logit)	48 v 40 (88)	0.52	0.54	NS
Fig. 18	Men Favored v Hampered	GEE (logit)	48 v 38 (86)	0.32	0.45	NS
Fig. 18	Men Hampered v Control	GEE (logit)	38 v 40 (78)	0.58	0.48	NS
Fig. 18	Women Favored v Control	GEE (logit)	52 v 35 (87)	0.61	0.25	NS
Fig. 18	Women Favored v Hampered	GEE (logit)	52 v 48 (100)	1.15	0.11	NS
Fig. 18	Women Hampered v Control	GEE (logit)	48 v 35 (85)	0.2	0.32	NS
Fig. 18	Men v Women Control	GEE (logit)	40 v 135 (175)	0.9	0.28	NS
Fig. 23A	Gender·Group·Key interaction	GLM (id)	261	1.76	0.17	NS
Fig. 23A	Men Up Key v Down Key	GLM (id)	63 v 63 (126)	-0.11	0.91	NS
Fig. 23A	Women Up Key v Down Key	GLM (id)	74 v 61 (135)	-1.046	0.29	NS
Fig. 23A	Favored Up Key v Down Key	GLM (id)	50 v 50 (100)	-1.191	0.23	NS
Fig. 23A	Control Up Key v Down Key	GLM (id)	44 v 31 (75)	0.95	0.34	NS
Fig. 23A	Hampered Up Key vs Down Key	GLM (id)	43 v 43 (86)	-0.29	0.76	NS
Fig. 23B	Gender·Group·Key interaction	GLM (id)	261	2.37	0.31	NS
Fig. 23B	Men Up Key v Down Key	GLM (id)	63 v 63 (126)	0.22	0.64	NS
Fig. 23B	Women Up Key v Down Key	GLM (id)	74 v 61 (135)	1.52	0.21	NS
Fig. 23B	Favored Up Key v Down Key	GLM (id)	50 v 50 (100)	2.83	0.09	NS
Fig. 23B	Control Up Key v Down Key	GLM (id)	44 v 31 (75)	0.55	0.46	NS

Figure	Comparison	Test	Sample size	Statistic	P-value	Code
Fig. 23B	Hampered Up Key vs Down Key	GLM (id)	43 v 43 (86)	0.32	0.57	NS
Fig. 24	Men v Women	GEE (logit)	28 v 28 (56)	0.30	0.59	NS
Fig. 24	Men v Women	Cox	28 v 28 (56)	-0.7	0.48	NS
Fig. 25A	Favoured v Control	GEE (logit)	94 v 107 (201)	0.48	0.52	NS
Fig. 25B	Phase 1 v Phase 2	GEE (logit)	252	2.24	1e-4	***
Fig. 26A	Solved Phase 1 v Unsolved Phase 1	GEE (logit)	201 v 56 (257)	2.35	2e-4	***
Fig. 26B	Phase 1 v Phase 2	GEE (logit)	252 v 56 (308)	0.97	0.75	NS

Table S1. Statistical tests breakdown. Logit and id (Gaussian) are link functions. GEE: General estimating equations. Cox: Proportional-hazards ratio model. GLM: Generalized Linear Model. All tests are two-sided. Statistics: Wald (GEE), Chi-squared (Interactions), Z normal (Cox and GLM). Significance code ***: < 0.001; **: < 0.01; *: < 0.05; NS: non-significant.

Mathematical Model

Control group

The experiment conducted for the Control group consists on a phase 1 'detached' from phase 2, since no SM is displayed. This way the probability of successful answer during the testing stage will be the same for the six stimuli presented. Then we can write the overall probability of successful answer at the testing trial *T* as

$$P(S=1)=\sum_{i=1}^{6} P_i(S=1)\cdot P(i\ appears\ at\ trial\ T) \qquad (26)$$

Since at any single trial all stimuli are equiprobable then $P(i\ appears\ at\ trial\ T)=1/6$. Besides $P_i(S=1)$ does not depend on the stimulus, so

$$P(S=1\,)=P_i(S=1)\sum_{i=1}^{6}\frac{1}{6}=P_i(S=1)\frac{1}{6}6=P_i(S=1)$$

and, from Eq. (25), the probability of successful answer at trial *T* for the Control group will be:

$$P_C(S=1)=\ 1-\frac{1}{2}\left(\frac{5}{6}\right)^{T-1}-\frac{1}{2}\left[(T-1)-\left(\frac{1-e^{-a(T-1)}}{e^a-1}\right)\right]\left(\frac{1}{6}\right)\left(\frac{5}{6}\right)^{T-2}$$

$$-\frac{1}{4}\left[(T-1)(T-2)-\frac{2}{(e^b-1)}\left[(T-1)-\left(\frac{1-e^{-b(T-1)}}{1-e^{-b}}\right)\right]\right]\left(\frac{1}{6}\right)^2\left(\frac{5}{6}\right)^{T-3} \qquad (27)$$

Favored group

According to the hypothesis, for Favored group the DMs of phase 2, here denoted by *i* = 1 and 2, were previously learned during the conditioning, after the SM was learnt. Therefore, when DMs appear during phase 2, the probability of successful answer will be always equal to 1.

This way the successful answer probability during the testing stage will be 1 for stimuli *i* = 1 and 2, and will be given by Eq. (25) for the remaining stimuli *i* = 3, …, 6. Thus considering again that, at any single trial, all stimuli are equiprobable, we can write the overall probability of successful answer at the testing trial *T* for the Favored group as

$$P_F(S=1)=\sum_{i=1}^{6} P_i(S=1)\cdot P(i\ at\ T)=\frac{1}{6}\sum_{i=1}^{6} P_i(S=1)$$

$$=\frac{1}{6}\left(1+1+\sum_{i=3}^{6} P_i(S=1)\right)=\frac{1}{6}\left(2+4P_i(S=1)\right) \quad (28)$$

Substituting Eq. (25) we obtain

$$P_F(S=1)=\ 1-\frac{1}{3}\left(\frac{5}{6}\right)^{T-1}-\frac{1}{3}\left[(T-1)-\left(\frac{1-e^{-a(T-1)}}{e^a-1}\right)\right]\left(\frac{1}{6}\right)\left(\frac{5}{6}\right)^{T-2}$$

$$-\frac{1}{6}\left[(T-1)(T-2)-\frac{2}{(e^{b}-1)}\left[(T-1)-\left(\frac{1-e^{-b(T-1)}}{1-e^{-b}}\right)\right]\right]\left(\frac{1}{6}\right)^{2}\left(\frac{5}{6}\right)^{T-3} \qquad (29)$$

Hampered group

Following the hypothesis, for Hampered group the DMs of phase 2, again denoted by *i* = 1 and 2, were previously wrongly learned during phase 1, i.e. the corresponding arrow key for the DMs is the opposite to that learned for the SM. Therefore the probability of successful answer when they appear for the first time during the testing stage will be equal to 0. When they appear for the second and successive times the new association rule will be learnt and the probability of successful answer will be given by Eq. (18). More in detail, let us consider the Eq. (14) for *i* = 1 and 2:

$$\begin{aligned}P_{1,2}(S=1) = {} & P_{1,2}(S=1\ \cap\ X_i=0)+\ P_{1,2}(S=1\ \cap\ X_i=1)+\ P_{1,2}(S=1\ \cap\ X_i=2)\\ & +\ P_{1,2}(S=1\ \cap\ X_i\geq 3)\end{aligned}$$

On the one hand

$$P_{1,2}(S=1\ \cap\ X_i=0)=P_{1,2}(S=1\ |X_i=0)\cdot P_{1,2}(X_i=0)=\ 0\cdot\left(\frac{5}{6}\right)^{T-1}=0 \qquad (30)$$

On the other hand the remaining terms $P_{1,2}(S=1\ \cap\ X_i=1)$, $P_{1,2}(S=1\ \cap\ X_i=2)$, and $P_{1,2}(S=1\ \cap\ X_i\geq 3)$ will be given respectively by Eq. (17), (22) and (24), so we get

$$P_{1,2}(S=1)=\ 1-\left(\frac{5}{6}\right)^{T-1}-\frac{1}{2}\left[(T-1)-\left(\frac{1-e^{-a(T-1)}}{e^{a}-1}\right)\right]\left(\frac{1}{6}\right)\left(\frac{5}{6}\right)^{T-2}$$

$$-\frac{1}{4}\left[(T-1)(T-2)-\frac{2}{(e^{b}-1)}\left[(T-1)-\frac{\left(1-e^{-b(T-1)}\right)}{1-e^{-b}}\right]\right]\left(\frac{1}{6}\right)^{2}\left(\frac{5}{6}\right)^{T-3} \qquad (31)$$

Considering then that $P_i(S=1)$ when *i* = 3, …, 6 is described by Eq. (25), we can write the overall probability of successful answer at the testing trial *T* for the Hampered group as

$$\begin{aligned}P_H(S=1) &= \sum_{i=1}^{6}P_i(S=1)\cdot P(i\ at\ T)=\frac{1}{6}\sum_{i=1}^{6}P_i(S=1)\\ &=\frac{1}{6}\left(\sum_{i=1}^{2}P_i(S=1)+\sum_{i=3}^{6}P_i(S=1)\right)\end{aligned}$$

so substituting and simplifying we obtain that

$$P_H(S=1) = 1 - \frac{2}{3}\left(\frac{5}{6}\right)^{T-1} - \frac{1}{2}\left[(T-1) - \left(\frac{1-e^{-a(T-1)}}{e^a - 1}\right)\right]\left(\frac{1}{6}\right)\left(\frac{5}{6}\right)^{T-2}$$

$$-\frac{1}{4}\left[(T-1)(T-2) - \frac{2}{(e^b-1)}\left[(T-1) - \left(\frac{1-e^{-b(T-1)}}{1-e^{-b}}\right)\right]\right]\left(\frac{1}{6}\right)^2\left(\frac{5}{6}\right)^{T-3} \quad (32)$$

In order to summarize the previous equations, we can write the successful answer probabilities at trial *T* for Favored, Control, and Hampered groups as:

$$P_F(S=1) = 1 - \frac{1}{3}\left(\frac{5}{6}\right)^{T-1}[1 + \alpha(a,T) + \beta(b,T)] \qquad (33)$$

$$P_C(S=1) = 1 - \frac{1}{2}\left(\frac{5}{6}\right)^{T-1}[1 + \alpha(a,T) + \beta(b,T)] \qquad (34)$$

$$P_H(S=1) = 1 - \frac{1}{2}\left(\frac{5}{6}\right)^{T-1}\left[\frac{4}{3} + \alpha(a,T) + \beta(b,T)\right] \qquad (35)$$

where

$$\alpha(a,T) = \left[(T-1) - \left(\frac{1-e^{-a(T-1)}}{e^a - 1}\right)\right]\left(\frac{1}{5}\right) \qquad (36)$$

$$\beta(b,T) = \frac{1}{2}\left[(T-1)(T-2) - \frac{2}{(e^b-1)}\left[(T-1) - \left(\frac{1-e^{-b(T-1)}}{1-e^{-b}}\right)\right]\right]\left(\frac{1}{5}\right)^2 \qquad (37)$$