Spike-based acquisition of grammatical structure: on the importance of low-level brain mechanisms for high-level cognitive skills

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Bei der Auswahl und Auswertung folgenden Materials haben mir die nachstehend aufgeführten Personen in der jeweils beschriebenen Weise ~~entgeltlich~~/ unentgeltlich geholfen.

1. Jutta L. Mueller*: Konzeptualisierung, Schreiben (kritische Beurteilung, Kommentare, Überarbeitung)
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3. *Manuskript "Spike-based statistical learning explains human grammar acquisition performance"

Weitere Personen waren an der inhaltlichen materiellen Erstellung der vorliegenden Arbeit nicht beteiligt. Insbesondere habe ich hierfür nicht die entgeltliche Hilfe von Vermittlungs- bzw. Beratungsdiensten (Promotionsberater oder andere Personen) in Anspruch genommen. Niemand hat von mir unmittelbar oder mittelbar geldwerte Leistungen für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen.

Die Arbeit wurde bisher weder im In- noch im Ausland in gleicher oder ähnlicher Form einer anderen Prüfungsbehörde vorgelegt.

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Zusammenfassung

Kognition kann entlang verschiedener Schnittstellen betrachtet werden. Hierbei hebt die ‘Gehirn-Kognition’-Schnittstelle das Ziel hervor, erklärende Modelle der Implementierung von Kognition im biologischen Gehirn zu formulieren. Darüber hinaus stellen die ‘niedrig-hoch’- und ‘subsymbolisch-symbolisch’-Schnittstellen die Bandbreite möglicher Arten kognitiver Repräsentation und Verarbeitung dar. Ziel der vorliegenden Thesis war es, mögliche Verbindungen zwischen diesen Schnittstellen zu identifizieren. Hierfür wurden die zugrunde liegenden Lernmechanismen des Erwerbs menschlicher Grammatik, einer hohen und potenziell symbolischen kognitiven Fähigkeit, tiefergehend betrachtet. Insbesondere für frühkindliche Phasen des Spracherwerbs werden assoziative und statistische Lernmechanismen als charakteristisch eingestuft. Diese Hypothese motivierte die Anwendung eines assoziativen, statistischen Lernmodells in einem event-basierten neuronalen Netzwerk, um das Erlernen isolierter und geschachtelter Grammatiken mit diskontinuierlichen Abhängigkeiten abzubilden. Die Lernleistung des Modells wurde anhand der resultierenden synaptischen Verbindungsgewichte ermittelt. Hierbei zeigte sich, dass dessen Verteilungen einer Reihe menschlicher Lernmuster entsprachen. Daher scheint assoziatives, statistisches Lernen einen wesentlichen Beitrag zum erfolgreichen Erlernen von Grammatik und möglicherweise auch von menschlicher Sprache zu leisten. Da es sich bei dem Lernmodell um einen subsymbolischen Mechanismus auf niedriger Ebene handelte, könnten hohes und symbolisches Lernen menschlicher Grammatik eine potenzielle subsymbolische Basis haben. Durch die Berücksichtigung von grundlegenden Komponenten und Verarbeitungsprinzipien des Gehirns, d.h. durch die Verwendung eines generischen rekurrenten neuronalen Netzwerks sowie verteilter Verarbeitung und unüberwachten Lernens, konnte ein mögliches minimales Set neurobiologischer Bedingungen für den Erwerb diskontinuierlicher Grammatiken identifiziert werden. Zusammengenommen wurde in dieser Thesis eine Verbindung zwischen den Forschungsfeldern der Psycho- und Neurolinguistik und der Neuroinformatik gefunden. Diese Verbindung wurde anhand der hervorstehenden Bedeutung von assoziativem, statistischem Lernen in beiden Feldern identifiziert. Das Modell beschreibt den speziellen Fall einer naiven, lernenden Person, die durch passive Exposition möglicherweise erste Erkenntnisse über die Statistiken der Umgebung erlangen könnte. Andere kognitive Mechanismen, die eventuell auf das so erlangte Wissen aufbauen, gehen wahrscheinlich über reines assoziatives, statistisches Lernen hinaus. Diese Thesis stellt deshalb einen möglichen Startpunkt für zukünftige Forschung dar, die einen Fokus auf das Zusammenspiel verschiedener kognitiver Strategien legt: angefangen bei subsymbolischem Lernen auf niedriger Ebene bis hin zu hoher, symbolischer Kognition.

Abstract

Cognition can be studied across a variety of interfaces. While the 'brain-cognition' interface highlights the aim to build explanatory models for the implementation of cognition in the biological brain, 'low-high' and 'subsymbolic-symbolic' interfaces demonstrate the scope of possible representation and computation types underlying cognition. This thesis aimed at contributing potential connecting links across these interfaces by taking a closer look at the underlying learning mechanisms of human grammar acquisition (i.e. a high-level and possibly symbolic cognitive skill). Motivated by the hypothesis that especially early childhood language acquisition phases are characterised by associative, statistical learning types, the acquisition of isolated and nested non-adjacent grammars was modelled by associative, statistical learning in a spiking recurrent neural network (i.e. a low-level and subsymbolic mechanism). By demonstrating that grammar learning outcomes of the model (i.e. distributed synapse assembly strengths) complied with a variety of grammar acquisition performance patterns of human learners, associative, statistical learning was identified as an essential contributor for successful grammar learning and potentially also language acquisition. Moreover, given that a low-level and subsymbolic mechanism accounted for aspects of high-level human grammar learning, this cognitive skill might potentially be grounded on a subsymbolic basis. Finally, by including core brain components and processing principles into the model (i.e. a generic recurrent neural network, distributed encoding and unsupervised learning), a potential minimal set of neurobiological requirements for non-adjacent grammar learning was identified. Taken together, this thesis provided a connecting link between the fields of psycho- and neurolinguistics and neuroinformatics that was identified by a salient commonality in both, namely the central role of associative, statistical learning. The model especially described how a naive learner might acquire first knowledge about the statistics of the surrounding environment by passive exposure. However, other cognitive mechanisms that potentially build up on the formed low-level knowledge representations might go beyond mere associative, statistical learning. This thesis therefore provided a potential starting point for future research with a focus on understanding in more detail the potential interplay of different cognitive strategies: starting from low-level and subsymbolic learning towards reaching high-level and symbolic cognition.

Contents

Chapter 1

From low- to high-level cognition

1.1 Cognition at several interfaces

1.1.1 The ‘brain-cognition’ interface

The identification of explanatory links between low-level neural mechanisms and high-level cognitive skills is a historically long-standing (Churchland and Sejnowski 1988; Milner et al. 1998; Albright et al. 2000) and until today one of the most challenging research endeavours of cognitive neuroscience (Kandel et al. 2013; Piccinini and Shagrir 2014; Amunts et al. 2016; Rolls 2021; Torres and Marro 2022; Urai et al. 2022). The ambitious aim to bridge the ‘brain-cognition’ interface has brought fourth major lines of research that are concerned with problems ranging from:

1. ‘Cognitive areas’, i.e. localising brain regions that are specific to cognitive functions (Strotzer 2009; Zilles and Amunts 2010; Judaš et al. 2012; Amunts and Zilles 2015; Snow 2016; Glasser et al. 2016; Fan et al. 2016),

2. ‘Functional networks’, i.e. characterising the interaction of cognitive brain regions within functional networks (Horwitz et al. 1999; Hagmann et al. 2008; Bressler and Menon 2010; Sporns 2013; Park and Friston 2013; Sporns 2014; Pulvermüller et al. 2014; Petersen and Sporns 2015; Smith 2016; Avena-Koenigsberger et al. 2018),

3. ‘Activity signatures’, i.e. correlating brain activity with behavioural and cognitive operations (Polich 1993; Buzsáki and Draguhn 2004; Poldrack et al. 2011; Arnal and Giraud 2012; Einevoll et al. 2013; Krakauer et al. 2017; Duncan et al. 2020; Urai et al. 2022), to

4. ‘Underlying mechanisms’, i.e. identifying neural and synaptic mechanisms that underlie information processing principles of the brain and ultimately also cognition (Sejnowski et al. 1988; Friston 2005; Markram 2013; Harris et al. 2019).

Creating a holistic understanding about the implementation of cognition in the brain certainly requires an integration across all these levels of investigation. Such integration might be outlined taking the neural underpinnings of language as an example. With regard to ‘Cognitive areas’, Broca’s area is well established as a central language processing and production region of the cerebral cortex (Geschwind 1970; Novick et al. 2010; Flinker and Knight 2018). Concerning ‘Functional networks’, Broca’s area is embedded in a larger scale language network (Hickok and Poeppel 2007; Friederici 2011; Fedorenko and Thompson-Schill 2014; Flinker et al. 2015; Ardila et al. 2016; Friederici et al. 2017) and thus interacts with other brain areas during the performance of linguistic operations like the parsing of syntax (Friederici et al. 2006; Chen et al. 2021). With respect to ‘Activity signatures’, oscillations or event-related potentials are correlated to the online dynamics of linguistic computation (Lau et al. 2008), as for example the mismatch negativity (Näätänen and Winkler 1999; Näätänen et al. 2007) that indicates the detection of grammatical rule violations (Mueller et al. 2012; Winkler et al. 2018a). Finally, research dedicated to ‘Underlying mechanisms’ provides conceptual (Garrido et al. 2009; May and Tiitinen 2010), probabilistic (Lieder et al. 2013) or mechanistic models (Wacongne et al. 2012) that explain how the mismatch negativity might arise. Despite these advances, the great ‘brain-cognition’ interface puzzle undoubtedly still misses a great amount of pieces for a further completion. This thesis aimed at contributing such a missing piece by investigating the relevance of low-level brain mechanisms for high-level cognitive skills. Being attributed to the above sketched research line ‘Underlying mechanisms’, this work was concerned with modelling the acquisition of grammatical structure of human language, i.e. a high-level cognitive skill, with spike-based statistical learning, i.e. a low-level brain mechanism. The methodology of this thesis was motivated by the idea that neuroscience has reached the so called ‘simulation phase’ (Fan and Markram 2019). This signifies that theoretical models of neural and synaptic information processing principles are now applicable for simulating brain function (Markram 2006; Kass et al. 2018; Einevoll et al. 2019) and, importantly, for testing their suitability as underlying computational modules of cognition (Kriegeskorte and Douglas 2018). Especially the continuous development of neural network simulation tools has paved the way towards this new ‘simulation phase’ (Diesmann and Gewaltig 2001; Natschläger et al. 2003; Migliore et al. 2006; Brette et al. 2007; Goodman and Brette 2008; Goodman and Brette 2009; Bekolay et al. 2014; Stimberg et al. 2014; Plotnikov et al. 2016; Tikidji-Hamburyan et al. 2017; Blundell et al. 2018; Stimberg et al. 2019). Their availability further advances the aim to formulate and test neurobiologically motivated cognitive models (Gerstner et al. 2012; Palm 2016) and thus, ultimately contributes towards make bridging the ‘brain-cognition’ interface possible.

1.1.2 The ‘low-high’ and ‘subsymbolic-symbolic’ debates

The ‘brain-cognition’ interface is not the only challenge to overcome. The aim to formulate neurobiologically motivated models of cognition inevitably leads to facing the ‘low-high’ and ‘subsymbolic-symbolic’ debates (Smolensky 1987; Smolensky 1988; Harnad 1990; Kelley 2003; Simen and Polk 2010; Smolensky 2012; Kriete et al. 2013; König et al. 2013; Werning et al. 2013; Dehaene et al. 2022). These deal with the central problem of elucidating the levels (i.e. ‘low-high’) or natures (i.e. 'subsymbolic-symbolic') of knowledge representations and cognitive operations. Here, mappings across a scale from low- to high-level are a common approach for distinguishing primarily sensory processes from cognitive operations (König et al. 2013; Dehaene et al. 2022). Across a scale from subsymbolic to symbolic, usually distributed and parallel or centralised and serial representation and operation schemes are contrasted (McClelland and Rumelhart 1985; Kelley 2003). Taken together, while neural representations of sensory inputs are primarily considered low-level and subsymbolic, cognitive skills like thought, reasoning or language are considered high-level and symbolic (Fig. 1.1). However, when trying to explain the emergence of symbolic cognition from distributed sensory or neural representations (Kriete et al. 2013; König et al. 2013; Butz 2016), the question arises if a mapping at theses extremes is mandatory? Or might aspects of high-level, symbolic cognition as well be explained by low-level and subsymbolic mechanisms? Especially when considering that cognition takes place in the neural substrate of the brain (Houdé and Tzourio-Mazoyer 2003; Barsalou 2008), it is nothing but reasonable to expect that low-level operation principles of neurons and synapses set important representational constraints and potentially also influence the outcome of subsequent, high-level cognitive performances. Therefore, next to the 'brain-cognition' interface, this thesis additionally dealt with understanding better to which degree low-level and subsymbolic brain principles might be relevant for high-level cognitive operations that are usually considered to be symbolic.

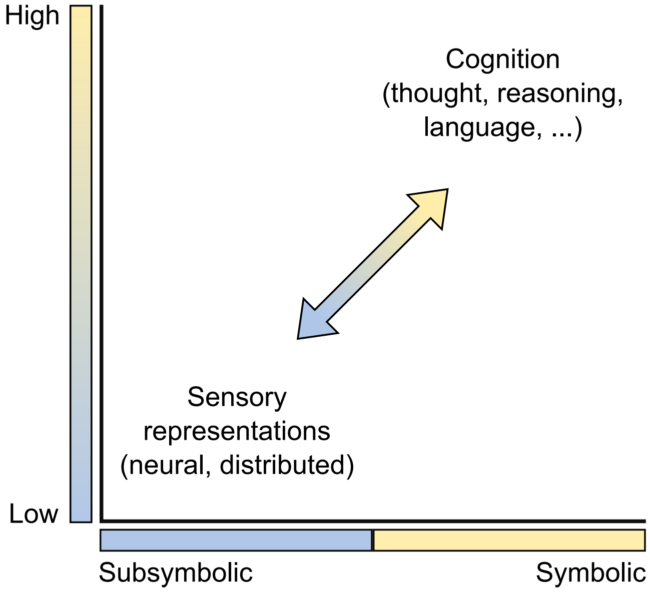


Figure 1.1: Cognition across 'low-high' and 'subsymbolic-symbolic' scales. Continuous 'low-high' scale and binary 'subsymbolic-symbolic' scale. Low-level and subsymbolic (blue) sensory representations (i.e. neural or distributed) contrast high-level and symbolic (yellow) cognition (i.e. thought, reasoning or language). Shaded double arrow indicates the missing link between the extremes of scales.

1.1.3 Challenges for a neuroscience of linguistics

While the 'brain-cognition' interface exists in any cognitive domain, it has specifically been described for the research areas of linguistics and neuroscience entitled as the 'interface problem' (Poeppel and Embick 2005). Here, the challenge to formulate a neuroscientific theory of linguistics was defined as a mapping problem between the 'elements' and 'operations' across domains (Fig. 1.2). According to the 'interface problem', elements and operations within domains can be related in causal ways while relations across domains remain random (Poeppel and Embick 2005; Embick and Poeppel 2015). To illustrate, in linguistics, the constituting elements of a language (i.e. its phonemes, syllables or words) are known to be subject to specific linguistic operations (i.e. parsing, generalisation or production). Equivalently, in neuroscience, core brain elements (i.e. neurons, synapses or networks) are known to perform certain operations (i.e. action potentials, oscillations or plasticity). However, linking 'elements' and 'operations' across domains is not trivial. Specifically, it is unclear to which degree or at which level of detail linguistic and neural elements and operations are related to each other (Poeppel 2012; Embick and Poeppel 2015; Friederici et al. 2017). For example, it is largely unknown at which elementary level a linguistic entity is neurally encoded (i.e. is a word reflected by individual neurons, dendrites or populations of cells?). Moreover, how linguistic operations relate to neural ones is mainly unidentified as well (i.e. is the production of an utterance supported by neural oscillations or individual action potentials?). These considerations reveal a general need for developing computational models of language that take neurobiological constraints of the brain into account (Poeppel and Embick 2005). Thus, by focusing on the implementation of language and speech in the brain (Petersson and Hagoort 2012; Poeppel 2014; Zuidema and Fitz 2019), the possibility to integrate basic neural principles with linguistic theory might arise (Jackendoff 2011). Finally, the 'interface problem' by Poeppel and Embick (2005) is a useful methodological scaffold for approaching the ambitious aim to overcome the 'brain-cognition' interface. It provides a strategy for identifying connecting links between neuroscience and cognition by motivating to search for shared principles across 'elements' and 'operations'.

1.2 From statistical regularity detection to language acquisition

1.2.1 Associative, statistical learning in early childhood

During early language acquisition, the primary source of information for a naive learner is the speech signal (Jusczyk and Luce 2002; Mueller et al. 2012; Mueller et al. 2018b; Frost et al. 2020). To illustrate, a pre-verbal newborn or child is constantly exposed to its first language by the utterances present in the surrounding environment. Moreover, as the sense of hearing develops before birth, both the exposure to spoken language and preliminary forms of language acquisition already start in utero (Gómez and Gerken 2000; Skeide and Friederici 2016; Minai et al. 2017). The speech signal is rich of temporal cues that are informative about specific

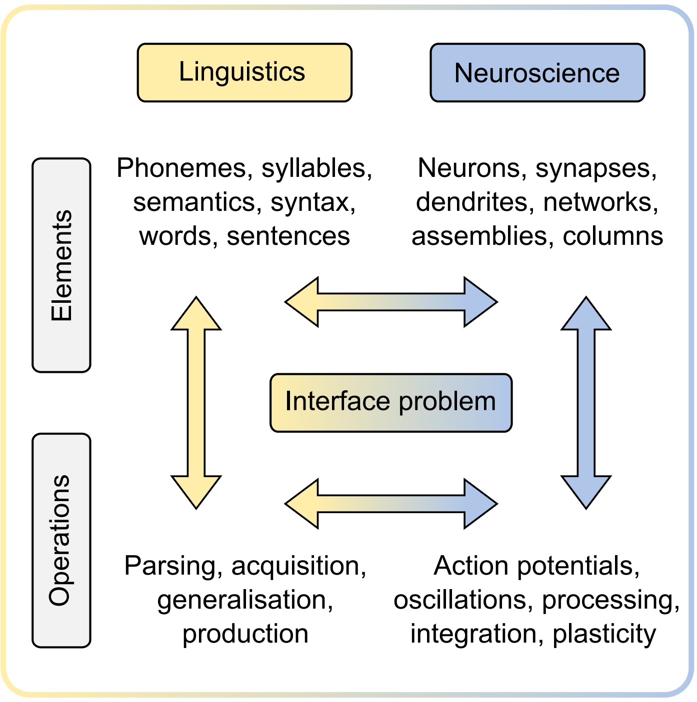


Figure 1.2: The 'interface problem' between linguistics and neuroscience. Elements and operations within each field can be related in explanatory ways (vertical arrows) while relations across the fields are random (horizontal arrows). Compare Fig. 7.1. in Poeppel and Embick (2005).

sound features and structures of a language (Rosen 1992). Further, the statistics of speech comprise a variety of distributional and conditional cues that are indicative for meaningful linguistic entities, i.e. words, or structural regularities, i.e. grammars (Thiessen and Erickson 2013b; Thiessen and Erickson 2013a; Saffran and Kirkham 2018; Frost and Monaghan 2020). Thus, the speech environment provides a bandwidth of information from which a language can be learned from scratch. Children show a remarkable sensitivity to the sound structures and statistics of speech, an ability which is therefore thought to help them bootstrapping a language's organisational principles (Johnson and Jusczyk 2001; Jusczyk 2002; Jusczyk and Luce 2002; de Diego-Balaguer et al. 2016). After their first year of life, children start to understand the communicative purpose of speech (Martin et al. 2012) and develop the ability to articulate words (O'Kane and Goldbart 1998). However, before speech production, there is a prolonged pre-verbal period in which children are exposed to their first language in a seemingly 'passive listening' way (Mueller et al. 2018a). Nonetheless, the importance of this phase becomes apparent when considering the variety of language-specific abilities that develop in this pre-verbal period. For example, newborns can discriminate different languages by their sound structures (Nazzi et al. 1998) and detect structural violations like backward pitch contours (Martinez-Alvarez et al. 2022). Further, pre-verbal children show preferences for repeating sound patters in their environment like their own names (Mandel et al. 1995). Moreover, also in foreign natural languages, pre-verbal children are able to discriminate familiar from novel words (Pelucchi et al. 2009) and detect grammatical rule violations (Friederici et al. 2011b). As the setting in which the language acquisition process begins is dominated by 'mere exposure' and 'passive listening' situations (Aslin 2017), underlying learning mechanisms were hypothesised to be 'implicit', 'automatic', 'statistical' or 'associative' (Perruchet and Pacton 2006; Erickson and Thiessen 2015; Saffran and Kirkham 2018; Mueller et al. 2018a). Summarised by the broad term 'statistical learning', a set of unsupervised learning principles is thought to enable the detection, extraction and ultimately the acquisition of statistical linguistic structures from the raw language signal (Romberg and Saffran 2010; Thiessen 2017). Of course, beyond 'mere exposure' and 'passive listening', pre-verbal children constantly interact with their environment, for example via the production of communication sounds like crying or babbling (Oller et al. 1976; Locke 1989; Cecchini et al. 2007; ter Haar et al. 2021). Yet, these types of verbal communication represent preliminary forms preceding the production of articulated speech (ter Haar et al. 2021). Presumably, when children start their first attempts to produce articulated speech, a transition from seemingly passive to interactive and feedback-guided acquisition phases is initiated. Here, for example, reinforcing feedback might be experienced intrinsically during the rewarding success of communicating a thought in a meaningful way (keyword 'reinforcement learning'). Or, in more supervised scenarios, external feedback by a teacher might guide language learning by providing a verbal correction of an otherwise ungrammatical utterance (keyword 'supervised learning'). However, such interactive learning settings and the possibility to refine language proficiency by specific feedback only occur after having passed through the pre-verbal and 'passive listening' developmental phase. Moreover, this transition of learning settings aligns to the developmental trajectory of cognitive control and the accompanying development of learning strategies. In early childhood, prefrontal cortex, a brain region responsible for cognitive control (Miller and Cohen 2001; Koechlin et al. 2003; Thompson-Schill et al. 2005; Novick et al. 2005), is immature and hence, uncontrolled and implicit learning strategies are hypothesised to dominate (Thompson-Schill et al. 2009). However, during prefrontal cortex maturation, a shift towards more goal-directed and controlled learning strategies occurs (Thompson-Schill et al. 2009). Applied to language acquisition, this developmental trajectory of prefrontal cortex is further hypothesised to explain observed shifts from automatic, associative language learning in infants and controlled learning in adults (Friederici et al. 2013; Mueller et al. 2018a). Recent findings further indicate that this shift presumably starts after the second year of life (Mueller et al. 2019; van der Kant et al. 2020; Paul et al. 2021). Even though infants outperform adults in passive listening language acquisition tasks (Mueller et al. 2018a), implicit learning is also present in adults (Friederici et al. 2002; Mueller et al. 2009; De Diego Balaguer et al. 2007; Morgan-Short et al. 2012). Thus, even though cognitively controlled learning strategies might become increasingly important in adulthood, statistical learning seems to be a mechanisms available throughout a lifetime. Taken together, the central role of associative, statistical learning during initial stages of language acquisition is underscored by pre-verbal children's sensitivity to statistical and linguistically meaningful information contained in the speech signal. Moreover, the predominance of 'passive listening' and 'mere exposure' learning scenarios in early developmental stages gives rise to the need of an unsupervised learning strategy.

Therefore, this thesis aimed at investigating more closely the scope and limits of cognitively low-level, associative, statistical learning in the specific context of early grammar acquisition.

1.2.2 Insights from artificial grammar learning

The role of associative, statistical language learning is commonly studied using the so called 'artificial grammar learning' (AGL) paradigm (Pothos 2007). A major motivation for the development of AGL was to study the processing and acquisition of specific linguistic entities or structures in isolation, i.e. without the biasing effect of a learner's individual level of language experience and proficiency (Petersson et al. 2012; Wilson et al. 2018; Uddén and Männel 2018). Though being criticised for not scaling up to the full complexity of natural languages (Beckers et al. 2012; Chen et al. 2021; Rawski et al. 2021), artificial grammars make use of the basic building blocks of language and therefore allow for a specific investigation of their processing and acquisition (Zuidema et al. 2020). Moreover, also in cognitive domains other than language, the application of artificial stimuli or tasks that contain isolated real-world features of interest is a well-established method for investigating central computational principles of cognition. For example, core mechanisms of vision and movement perception are studied using moving bars or animated images (Castet and Masson 2000; Cracco et al. 2021). Here, basic principles of real-world vision were elucidated by low-dimensional, artificial screen stimuli. But also higher-order cognitive functions like problem solving are investigated by well-defined, artificial toy problems (Dörner and Funke 2017). In the case of language research, artificial grammars are constructed 'miniature languages' composed of linguistic acoustic items, for examples syllables that do not exist in natural language (Wilson et al. 2018). Training procedures according to the AGL paradigm usually comprise the exposition of a passive listener to an acoustic stimulus stream that contains the grammar. Here, a common technique is the so called 'oddball training' where invalid or ungrammatical exemplars, i.e. low-frequent deviants, are interspersed randomly into a stream of otherwise valid or grammatical exemplars, i.e. high-frequent standards (Sussman 2007). Implicit learning performances are measured by behavioural responses like head-turn preferences in children (Kemler Nelson et al. 1995), even though a large variety of preference directions along the developmental trajectory has to be taken into account (Culbertson et al. 2016; Santolin et al. 2020). However, also instructed forms of grammaticality judgements (Chen et al. 2021) and free recall techniques exist (Kidd et al. 2020; Isbilen et al. 2020). Further, brain signatures like the mismatch negativity in response to deviant stimuli (Näätänen and Winkler 1999; Näätänen et al. 2005; Näätänen et al. 2007; Kuhl and Rivera-Gaxiola 2008) are interpreted as a sign of error detection (Sussman 2007; May and Tiitinen 2010). While in adults, mismatch potentials are characterised by negativity, in children both negativity or positivity occur (Trainor et al. 2003; He et al. 2007). The AGL paradigm provided major insights into early statistical language acquisition. In preverbal children, observed learning abilities ranged from the segmentation of words (Saffran et al. 1996a; Aslin et al. 1998), tone sequences (Saffran et al. 1999) to the acquisition of grammatical rules or syntax (Marcus et al. 1999; Saffran and Wilson

2003). However, also verbal children and adults showed implicit learning successes in word segmentation (Saffran et al. 1996b; Saffran et al. 1997) and grammar acquisition (Reber 1967; Thompson and Newport 2007; Kidd 2012). Taken together, these findings by AGL demonstrate the importance of implicit and statistical learning for non-proficient but also proficient language learners to acquire knowledge about the basic units of language, namely its words and grammars. Moreover, statistical learning was also demonstrated for artificial visual scenes in both children (Fiser and Aslin 2002b; Kirkham et al. 2002) and adults (Fiser and Aslin 2002a; Fiser and Aslin 2005; Lazartigues et al. 2021) but also for tactile sequences (Conway and Christiansen 2005). The demonstration of statistical learning across modalities therefore suggests the existence of domain-general, statistical learning mechanisms for general sensory scene understanding (Conway and Christiansen 2005; Frost et al. 2015) beyond the scope of language acquisition.

1.2.3 Non-adjacent dependency acquisition

Language is rich of discontinuous relations among its constituting units. In this regard, non-adjacent dependencies (NADs) are prominent discontinuous grammars where related elements are separated by intervening material (Wilson et al. 2018). For example, in tense agreement, the '*is, -ing*' frame represents an isolated NAD that is combinable with arbitrary verbs, resulting in the grammatical structure '*is* [verb]*ing*' (Wilson et al. 2018). Moreover, mastering NADs is important for understanding nested sentences (de Vries et al. 2012), as for example '*the boy* [the girl chased] *kicked the ball*', where the outer sentence, i.e. 'the boy kicked the ball', is wrapped around the inner embedded clause, i.e. 'the girl chased' (Winkler et al. 2018a). Both isolated and nested NADs pose the challenging task for a learner to detect the grammatical relation between the non-adjacent elements while omitting the intervening material (Wilson et al. 2018). Despite this complexity of the problem, NAD learning in natural language has been observed already in 4-month-olds (Friederici et al. 2011b) and 18-month-olds (Santelmann and Jusczyk 1998; Höhle et al. 2006). Moreover, also nonlocal rules of syntax were already acquired by 18-month-olds (Perkins and Lidz 2021). Using artificial grammars, the ability to acquire NADs was shown for 8-month-olds (Kabdebon et al. 2015), 15-month-olds (Gómez and Maye 2005), 17-month-olds (Frost et al. 2020) and 18-month-olds (Gómez 2002). Further, NAD learning was not restricted to the language domain but could be demonstrated for other modalities like tone sequences in 5-month-olds (Winkler et al. 2018a; Winkler et al. 2018b), human action sequences in 9-month-olds (Lu and Mintz 2021) and visual sequences in 13- to 15-month-olds (Bettoni et al. 2021). But also in adults, the implicit acquisition of linguistic NADs could be evoked by passive listening training procedures (Perruchet et al. 2004; De Diego Balaguer et al. 2007; van den Bos et al. 2012; Romberg and Saffran 2013; Grama et al. 2016; Frost and Monaghan 2016; Isbilen et al. 2022). Again, also adults could learn NADs in other modalities like tone sequences (Gebhart et al. 2009; Endress 2010) and visual symbols (Bahlmann et al. 2009; Iao et al. 2021). Throughout, a variety of stimulus conditions for the facilitation of artificial NAD acquisition has been identified ranging from statistical, i.e. distributional and conditional, to perceptual stimulus features (Wilson et al. 2018). For example, a high variability of the intervening material was beneficial for NAD learning by facilitating a detection of the statistically more persistent, invariant non-adjacent relations (Gómez 2002; Gómez and Maye 2005). But also in general, high frequent linguistic structures or words seem to be valuable cues for learning and efficient processing (Mintz 2003; Brysbaert et al. 2018). Further, training procedures with an incremental transition from adjacent to non-adjacent dependencies were beneficial (Lany and Gómez 2008). In this context, learning grammatical dependencies of short length is generally thought to be easier because less intervening material has to be processed (van den Bos and Poletiek 2008). Next, pauses between grammar exemplars were beneficial as they introduced segmental cues that facilitated their detection (Peña et al. 2002; Mueller et al. 2010; de Diego-Balaguer et al. 2015). But also in natural language, pauses were valuable cues for the detection of phrase boundaries (Männel and Friederici 2009). Further, a bandwidth of structural features were identified to facilitate NAD learning by emphasising the discontinuous relations. For example, NAD acquisition was facilitated when grammatical elements were perceptually similar (Newport and Aslin 2004), shared phonological (Onnis et al. 2005) or prosodic features (Grama et al. 2016) or were marked by prosodic cues (Mueller et al. 2010). Finally, evoked directed attention on NADs facilitated their acquisition (Pacton and Perruchet 2008; de Diego-Balaguer et al. 2016). Despite these insights, it remained unclear whether improved NAD acquisition performances in response to this variety of stimulus conditions could be explained by a shared underlying learning mechanism. Here, the claim that statistical, associative learning is a predominant learning type for the acquisition of language would gain further support if it could explain this variety of observations. Motivated by the need to further evaluate the performance and explanatory power of associative, statistical learning (Frost et al. 2019; Bogaerts et al. 2021), this thesis took the identified stimulus variations ranging from variability, dependency length, stimulus pauses to emphasis on grammars (Wilson et al. 2018) as benchmark conditions for this endeavour. Further, beyond isolated NADs (Wilson et al. 2018) also the acquisition of nested NADs (Winkler et al. 2018a) was studied under these stimulus constraints.

1.3 Brain principles for neuro-cognitive models

1.3.1 Which brain features to consider?

A major question for the development of neurobiologically grounded models of cognition is the identification of indispensable brain components and operation principles. In other words, what are the neural constraints that are essential for building mechanistic models of cognition (O'Reilly 1998; Eliasmith 2007; Maass 2016; Pulvermüller et al. 2021; Saxe et al. 2021)? The bandwidth of potential architectural structures, encoding and learning schemes is large. To illustrate, should neuro-cognitive models consider the columnar layout of cortex (Markram 2006; DeFelipe et al. 2012), include several neural layers (LeCun et al. 2015; Richards et al. 2019) or implement recurrent connectivity schemes (Kietzmann et al. 2019; van Bergen and Kriegeskorte 2020; Prince et al. 2022)? Are specific large-scale networks (Eliasmith and Trujillo

2014; Markram et al. 2015; Abdellah et al. 2017) required or can generic small-scale networks (Miner and Triesch 2016) be cognitively functional? Can the morphology of biological neurons be compressed to point models (Izhikevich 2004) or do we miss out an essential part of neural computation by neglecting the complex structures of dendritic trees (Frick and Johnston 2005; Spruston 2008; Stuart and Spruston 2015; Hawkins and Ahmad 2016; Doron et al. 2017; Bono and Clopath 2017; Kanari et al. 2022)? Is the precise timing of individual action potentials of relevance (Gerstner et al. 1993; Gerstner et al. 1997; Borst and Theunissen 1999; VanRullen et al. 2005; Panzeri et al. 2014; Fiorillo et al. 2014; Nolte et al. 2019) or are firing rates (Stemmler and Koch 1999; Heiberg et al. 2018; Keeley et al. 2019; Qian and Zhang 2020) and oscillations (Buzsáki and Draguhn 2004; Siegel et al. 2012; Kayser et al. 2012; Heusser et al. 2016; Kühn and Helias 2017) the main carriers of information? And finally, are bottom-up local learning rules (Markram et al. 2011) or top-down error- and reward-driven learning schemes (Khaligh-Razavi and Kriegeskorte 2014; Yamins and DiCarlo 2016; Kriegeskorte and Golan 2019) at the heart of cognition? An expedient approach to overcome this multitude of possibilities and options is to concentrate on the nature of the task of interest, followed by a subsequent search of a minimal set of brain features that are potentially supportive (Abbott 2008). For example, if the question is how brain signatures like the mismatch negativity arise, models with continuous encoding schemes potentially represent reasonable substrates as they produce oscillatory outputs that correspond to the experimentally observed signal (Lieder et al. 2013). Further, if the question is how the interaction of a learner with the environment shapes knowledge representations, reinforcement schemes are probably the learning type of choice (Clay et al. 2021). Thus, decisions about included biological detail in model architectures and about the applied encoding or learning schemes ideally relate to the constraints given by the research question. However, this approach inevitably introduces strong biases by considering specific brain and hence model features to be appropriate or supportive a priori. Still, a successful reproduction of the phenomenon of interest by the chosen feature set can be viewed as a major milestone for a further refinement of indispensable neuro-cognitive model properties in the specifically defined context (Abbott 2008; Stöckel et al. 2021). Finally, models at all levels of biological detail ranging from single neuron outputs to mass signals have their reasons as they merely reflect the large diversity of brain features and operations that exist and hence, the bandwidth of analysis levels at which brain dynamics and cognition can be described and studied (Deco et al. 2008; Panzeri et al. 2015). In this thesis, the search of an appropriate neural modelling substrate was guided and facilitated by considering a top-down constraint from experimental sciences (Eliasmith and Trujillo 2014), namely the associative language learning hypothesis (Mueller et al. 2018a; Thompson-Schill et al. 2009). Interestingly, associative learning in the form of spike-timing dependent plasticity (STDP) is considered a central unsupervised learning scheme of the brain (Markram et al. 1997; Bi and Poo 1998; Bi and Poo 1999; Markram et al. 2011). This salient commonality between significant learning types in linguistics and neuroscience motivated to explore the power of STDP for potentially explaining the associative acquisition of grammatical structures like NADs. Choosing associative, statistical learning by STDP as the algorithm of interest further entailed the use of a spike-based recurrent neural architecture for its implementation (Gilson et al. 2010; Kunkel et al. 2011). Taken together, in this thesis, the minimal set of potentially supportive brain features for associative grammar acquisition therefore consisted of spike-based statistical learning in a recurrent neural network.

1.3.2 Spike-based encoding and processing

Biological brains encode and transmit information in a striking way that relies on the interplay between continuously evolving neuronal or synaptic parameters and discontinuous all-or-nothing events, i.e. action potentials or spikes (Stevens and Zador 1995; Strong et al. 1998; Borst and Theunissen 1999; Aur et al. 2006). Here, continuous variables like the membrane potential of a neuron or the plastic weight of a synapse are thought to reflect the integrated input received over time (Maass and Markram 2002). Complementary, spikes encode currently processed stimuli or reflect the current activity output of neurons (Nádasdy 2000). Next to the internal dynamics of continuous variables, for example decaying (i.e. leaking) or consolidation behaviours (Zenke et al. 2013), they undergo local and instantaneous spike-triggered changes that drive activity, processing and ultimately also learning (Stimberg et al. 2014). Considering this dynamic interaction of variables at different temporal scales, the importance of time for neural encoding, processing and computation becomes highlighted (Maass 1997; Belatreche et al. 2007). Many temporal codes are observed in neurons, ranging from bursting behaviours (Izhikevich 2003; Izhikevich 2006; Berger et al. 2010), synchrony (Engel et al. 1991; Engel et al. 1992; König et al. 1996; Stevens and Zador 1998; Uhlhaas et al. 2009; Pipa and Munk 2011; Singer and Lazar 2016; Palacios et al. 2019; Lewis et al. 2021), asynchrony (Ostojic 2014), sparse coding (Olshausen and Field 2004; Hromádka et al. 2008; Koulakov et al. 2009; Kloppenburg and Nawrot 2014) to distributed spatio-temporal patterns (Gerstner et al. 1993; Nádasdy 2000; Shamma 2001; Fellous et al. 2004; Plenz and Thiagarajan 2007; Pillow et al. 2008; Kayser et al. 2009; Buonomano and Maass 2009; De Zeeuw et al. 2011; Ju et al. 2015; Takahashi et al. 2015). Potentially, this flexibility of a spike-based neural code is the brain's way to represent the rich temporal structures encountered in its sensory environment (Gerstner et al. 1997; deCharms and Zador 2000; Panzeri et al. 2010). Speech is a prime example of such a temporal environmental signal, unfolding sequentially and embedding a diversity of structured cues (Rosen 1992). Notably, the encoding of sound and speech comprises a locking of neurons' excitability or oscillatory activity to the temporal contours of the acoustic envelope in humans (Peelle and Davis 2012; Giraud and Poeppel 2012; Ding and Simon 2014; Doelling et al. 2014; Ding et al. 2016; Teng et al. 2017; Keitel et al. 2018; Kaufeld et al. 2020). Further, sampling windows at different time scales underlie online speech understanding (Poeppel 2003; Luo and Poeppel 2007; van Wassenhove et al. 2007; Poeppel et al. 2008; Norman-Haignere et al. 2022; Schmitt and Obleser 2022). But also in monkeys, this temporal locking to the acoustic stimulus is observed (Lakatos et al. 2005). Moreover, at the spike-based level, the temporal tracking of acoustic stimulus properties is a universal neural processing feature as demonstrated in rats (Machens et al. 2004), songbirds (Narayan et al. 2006) monkeys (Belitski et al. 2010; Brasselet et al. 2012; Ng et al. 2013) and bats

(García-Rosales et al. 2018). The spike-based temporal coding of biological neurons has a long history of being simulated by the model class of leaky integrate-and-fire (LIF) neurons (Abbott 1999; Izhikevich 2004; Brette and Gerstner 2005; La Camera et al. 2006; Brunel and van Rossum 2007; Pospischil et al. 2008). This class implements the above sketched hybrid system of a continuously evolving variable, i.e. the leaky integrator, in combination with the discontinuous generation of spike events (Stimberg et al. 2014). Importantly, LIF neurons do not model the voltage trace of action potentials explicitly but rather define spikes by their time points of occurrence (Maass 1997). Beyond modelling the processing dynamics of individual cells, LIF neurons allow to investigate spike-based activity dynamics and processing principles also at the network level (Izhikevich 2003; Scarpetta and de Candia 2013; Abbott et al. 2016; Sahasranamam et al. 2016; Duarte and Morrison 2019). Therefore, they are an important research tool for understanding the details of neural computation (Kass et al. 2018) but also for testing the implementation of high-level cognitive skills in a low-level and distributed neural substrate (Vogels and Abbott 2005; Vertes and Duke 2010; Duarte et al. 2018).

1.3.3 Local synaptic and neural plasticity

Time is also essential for local learning at individual synapses (Fuhrmann et al. 2002). Here, the relative timing between pre- or postsynaptic input events is decisive for the direction and degree of plasticity changes as evidenced by electrophysiological measurements in rat cortical neurons (Markram et al. 1997; Bi and Poo 1998; Debanne et al. 1998; Bi and Poo 1999; Feldman 2000; Sjöström et al. 2001; Froemke and Dan 2002). The collected findings of these experiments further gave rise to the development of computational models of spike-timing dependent plasticity (Song et al. 2000; Rubin et al. 2001; Izhikevich and Desai 2003) that include the following learning principles. First, STDP induces a strengthening for temporally positive correlations (i.e. potentiation by *pre-post* events) and a weakening for temporally negative correlations (i.e. depression by *post-pre* events) at synapses (Bi and Poo 1998). This plasticity profile of STDP is widely thought to support the theory of 'Hebbian learning' (Abbott and Nelson 2000; Markram et al. 2011; Markram et al. 2012) according to which positively correlated event sequences between two neurons elicit a strengthening of their synaptic connection (Hebb 1949). However, also a bandwidth of other temporal windows exists, demonstrating the variety of temporal learning algorithms that can be expressed locally at biological synapses (Kepecs et al. 2002; Shouval et al. 2010; Graupner and Brunel 2012a). Second, temporal windows for the induction of potentiation and depression are characterised by exponential contours (Dan and Poo 2006; Markram et al. 2011). Thus, the extent of plasticity changes increases with temporal proximity of events and respectively decreases with temporal distance. And finally, STDP is frequency dependent (Markram and Tsodyks 1996; Markram et al. 1998b; Markram et al. 1998a). In STDP models, this is expressed by a positive correlation of weight changes to stimulus frequency (Graupner and Brunel 2012a; Litwin-Kumar and Doiron 2014; Zenke et al. 2015). Model implementations of STDP usually comprise spike-triggered, exponentially decaying memory traces whose time constants define the temporal windows of plasticity induction. These memory traces are a computationally affordable way for implementing the STDP windows. However, they are rather theoretical constructs, i.e. do not reflect a specific parameter of biological synapses. This highlights the phenomenological character of STDP models (Morrison et al. 2008) that reproduce the plasticity outcome at synapses but not necessarily the underlying, biophysical signalling dynamics. Still, memory traces based on biophysical pathways exist, as for example in calcium-based STDP models (Shouval et al. 2002; Graupner and Brunel 2010; Graupner and Brunel 2012a; Graupner and Brunel 2012b). Taken together, STDP is a phenomenological, associative and statistical learning model that describes how the connection strengths, i.e. synaptic weights, between neurons are shaped during online spike-based processing. It represents a domain-general learning algorithm of the brain and allows to study the emergence of synaptic weight memory (Martin et al. 2000; Abbott and Regehr 2004; Hu et al. 2016) and cortical map formation (Song and Abbott 2001; Kepecs et al. 2002). However, synaptic weights are not the only brain parameters that can undergo plasticity changes. Also structural plasticity, i.e. the growth and vanishing of synaptic connections (Le Bé and Markram 2006) is considered a possible mechanism of learning and memory in the brain (Miner and Triesch 2016; Gallinaro et al. 2022). Moreover, also neurons demonstrate an activity-dependent intrinsic plasticity (IP) of their excitability thresholds (Turrigiano et al. 1994; Desai et al. 1999; Daoudal and Debanne 2003). In IP models, the voltage threshold for spike generation usually increases in response to each emitted spike and decreases during periods of neuronal silence (Lazar et al. 2009; Stimberg et al. 2014). Thereby, as highly active neurons subsequently have to reach higher sub-threshold activity states in order to emit a spike, IP contributes to firing rate homeostatis and the stabilisation of network activity (Lazar et al. 2007). Further, the decay of excitability thresholds during silence allows for a redundant utilisation of a network's resources as it facilitates the participation of previously inactive neurons (Toutounji and Pipa 2014). Taken together, the activity-dependent history of processed stimuli can also be imprinted neurally by the plasticity of excitability thresholds (Daoudal and Debanne 2003; Zhang and Linden 2003). However, IP is commonly applied as a complementary mechanism next to learning via synaptic weight plasticity (Lazar et al. 2009; Triesch 2004; Lazar et al. 2007; Triesch 2007; Toutounji and Pipa 2014; Leugering and Pipa 2018). In this thesis, the combination of synaptic STDP and neural IP therefore represented the scaffold of choice for exploring associative, statistical learning in a spike-based neural network model.

1.3.4 Recurrent assemblies for cognition

Recurrent connectivity of excitatory and inhibitory neurons is a predominant architectural feature of the cortex (Douglas et al. 1989; Thomson and Deuchars 1994; Douglas et al. 1995a; Thomson and Bannister 2003; Binzegger et al. 2004; Markram et al. 2004; Douglas and Martin 2004; Douglas and Martin 2007a; Reimann et al. 2017a; Siu et al. 2022). Given its ubiquitous presence, generic recurrent networks are considered basic computational units of the brain (Shu et al. 2003; Kalisman et al. 2005; Douglas and Martin 2007b; Perin et al. 2011). Further, in combination with associative STDP, recurrent excitatory networks are viewed as suitable neural substrates for the formation and representation of distributed memory (Mishra et al. 2016; Kossio et al. 2021). Here, the plasticity-driven emergence of strongly connected subgroups in the excitatory network is thought to underlie the formation of functional circuits, also referred to as ‘Hebbian cell assemblies’, that serve the purpose of stimulus-specific feature encoding (Pulvermüller 1996; Chady 2001; Reilly 2001; Sommer and Wennekers 2003; Lansner 2009; Huyck and Passmore 2013; Palm et al. 2014; Poo et al. 2016). At the activity level, cell assemblies demonstrate correlated dynamics (Peyrache et al. 2010; Reimann et al. 2017b) or attractor states (Amit et al. 1997). However, when structural plasticity is subject to learning, also silent memories can emerge (Gallinaro et al. 2022). Beyond being a potential substrate for neural information encoding (Wehr and Laurent 1996; Sakurai 1999), assemblies are also thought to support higher cognitive function (Buzsáki 2010; Pulvermüller et al. 2014; Müller et al. 2020). For example, in language they are hypothesised to underlie the encoding and processing of words (Wennekers et al. 2006) or syntax (Wennekers and Palm 2009; Papadimitriou et al. 2020). Building up on these ideas of assembly-based cognition, this thesis investigated the plasticity-driven emergence of synapse assemblies in the excitatory-to-excitatory connections of a recurrent neural network. By reading from the synaptic weight distribution (Barbour et al. 2007) after learning, the ability of the model to encode NADs by synapse assemblies was evaluated.

Chapter 2

The potential of spiking neural networks

2.1 From brain principles to cognition

2.1.1 Spike-based models of brain properties and dynamics

The motivation to consider spiking neural networks as promising modelling substrates for explaining cognitive computations is based on the bandwidth of brain properties and dynamics that they reproduce. Spiking models predominantly cover the previously identified abstraction levels ‘Functional networks’, ’Activity signatures’ and ‘Underlying mechanisms’ of the ‘brain-cognition’ interface. For example, regarding ‘Functional networks’, the dynamics of the thalamo-cortical system were modelled at a large scale (Izhikevich and Edelman 2008) and the filter properties of the thalamus further classified (Connelly et al. 2016). At the ‘Activity signature’ level, spiking networks reproduced cortical resting activity (Deco and Jirsa 2012; Deco et al. 2013), generated a large bandwidth of cortical oscillation types (Izhikevich 2006) or provided explanatory links between spiking activity and cortical oscillations (Vincent-Lamarre et al. 2020). Further, they modelled local field potentials (Reimann et al. 2013) and electroencephalography (EEG) data (Doborjeh et al. 2019; Schwab et al. 2021). At the ‘Underlying mechanisms’ level, spiking models explained basic brain properties like the self-organisation into receptive fields (Izhikevich et al. 2004), the emergence of synaptic inhomogeneities (Effenberger et al. 2015) and principles of information transfer (Zajzon et al. 2019). But also binary models, i.e. approximations of spiking models, could further elucidate principles of neural information transmission (Del Papa et al. 2017) and computation performance (Toutounji and Pipa 2014). Beyond, cortical rewiring was modelled by binary and spike-based structural plasticity (Zheng et al. 2013; Miner and Triesch 2016). Additionally, the role of spike-based structural plasticity for stable memory formation (Gallinaro et al. 2022) expanded research concerned with spiking learning and memory models grounded in synaptic weight plasticity (Zenke et al. 2015). Spiking models further modelled working memory (Szatmáry and Izhikevich 2010; Mi et al. 2017) and reproduced cortical sequence learning (Klos et al. 2018) observed in rats (Xu et al. 2012). In the context of sensory perception and cognitive science research, spiking approaches achieved the modelling of auditory adaptation in general (Kudela et al. 2018) and during oddball training (Mill et al. 2011) as well as the modelling of mismatch negativity (Wacongne et al. 2012). Further, spiking models were used to elucidate how the discrepancy between the different time scales of behaviours, i.e. taking place at the order of seconds, and neural dynamics, i.e. taking place at the order of milliseconds, might be bridged (Melamed et al. 2004; Setareh et al. 2018). Taken together, the spiking models collected here demonstrate the great flexibility of this model class for reproducing and explaining brain properties and dynamics in a variety of contexts.

2.1.2 Spike-based models of cognition

Even though a large bandwidth of brain properties and dynamics were reproduced by spiking models, spike-based approaches for the modelling of high-level cognitive skills remain rare. However, a small-scale model for the implementation of spike-based numerical cognition was proposed (Rapp et al. 2020) as well as a very large-scale spiking model for solving several cognitive tasks (Eliasmith 2005; Eliasmith et al. 2012; Stewart et al. 2012). These approaches provide first indications about a general feasibility of implementing cognitive skills in spiking neural networks. However, the extent to which this model class is applicable to explaining high-level cognition in a broader sense has not been demonstrated in a satisfying manner yet. Taken together, a bottom-up approach for accomplishing the transition from 'spiking models of brain dynamics' to 'spiking models of cognition' seems to remain a major open research problem. However, potentially, a top-down transition approach from 'non-spiking models of cognition' to spiking ones might provide valuable contributions. For example, especially the class of deep neural networks successfully implement cognitively relevant functions ranging from pattern detection in speech and vision (LeCun et al. 2015) to cognitive planning and navigation (Cichy and Kaiser 2019). Interestingly, a large bandwidth of studies already explored the possibility to consider spike-based encoding schemes of the brain also in deep neural architectures (O'Connor and Welling 2016; Neil et al. 2016; Lee et al. 2016; Bellec et al. 2018; Park et al. 2019; Wu et al. 2019; Sengupta et al. 2019; Bellec et al. 2020; Han and Roy 2020; Kaiser et al. 2020; Wu et al. 2020; Zhang et al. 2020a; Zhang and Li 2020; Jia et al. 2021; Ma et al. 2021; Tang et al. 2022). Here, spike-based processing and learning were considered potential solutions for solving efficiency problems in deep architectures that are introduced by resource extensive update cycles (Neil et al. 2016; Lee et al. 2016; Park et al. 2019; Wu et al. 2020; Zhang et al. 2020a). Further, spiking neurons were widely viewed as an important model feature to improve 'biological realism' (Pfeiffer and Pfeil 2018; Sengupta et al. 2019; Jia et al. 2021; Tang et al. 2022). Finally, these approaches already reached benchmark (Wu et al. 2019; Ma et al. 2021) or even better learning performances as compared to the state-of-the-art (Sengupta et al. 2019; Jia et al. 2021). Taken together, the challenge to build spiking models of higher-order cognition might profit from integrating key insights gained by both modelling fields that either deal with primarily biologically motivated or deep artificial neural networks (Pfeiffer and Pfeil 2018; Taherkhani et al. 2020; Rapp and Nawrot 2020; Macpherson et al. 2021; Eshraghian et al. 2022).

2.2 From sequence to language learning models

2.2.1 Sequence learning as a prerequisite for language

The sequential nature of language poses the challenging task to extract grammatical structures during online processing (Mueller et al. 2012; Christiansen and Chater 2016; Mueller et al. 2018a). Further, linguistic dependencies are considered to be sequential to a great extent so that, as a consequence, language understanding, learning and production might be well described as sequence solving problems (Frank et al. 2012). Going in line with this idea, also this thesis hypothesised that language acquisition might substantially rely on general temporal sequence processing and learning abilities. However, language can also be described as highly hierarchical with tree-like dependency structures amongst linguistic elements or categories that go beyond mere sequential relations (Makuuchi et al. 2009; Friederici et al. 2011a; Jäger and Rogers 2012; Fitch and Friederici 2012; Beekhuizen et al. 2013; Yang et al. 2017; Uddén et al. 2020; Chen et al. 2021). Acknowledging this, sequence learning can nonetheless be considered an essential underlying skill of hierarchical linguistic parsing. Moreover, it potentially is a crucial prerequisite for mastering the complexity of human language. For example, while the parsing of syntax in a sentence might require hierarchical analysis strategies (Dehaene et al. 2015; Doumas and Martin 2018; Chen et al. 2021), sequential processing abilities are indispensable for the extraction of the linguistic structures of interest that are embedded in the temporally unfolding language signal (Frank et al. 2012; Martin and Doumas 2017; Uddén et al. 2020). Taken together, understanding better how sequential and hierarchical aspects of language and the respective cognitive analysis strategies for parsing combine represents a major open research challenge (Dehaene et al. 2015). As the aim of this thesis was to elucidate possible low-level and neural mechanisms underlying grammar learning during online processing, the focus was primarily set on sequence processing, learning or production skills. Further, these were not necessarily required to be language-specific, but could rather be domain- or modality-general. To illustrate, they might include behavioural or cognitive capacities ranging from movement generation (Doyon 2008), olfactory (Johnson et al. 2013), tactile (Bale et al. 2017) and visual sequence learning (Bettoni et al. 2021) to counting (Zaleznik and Park 2021). Though modality-specific constraints were identified (Conway and Christiansen 2005), especially integration in visuo-auditory (Bröhl et al. 2022) and auditory-tactile domains (Bresciani et al. 2005) highlighted tight links between sequence processing abilities across the senses. Thus, by looking for mechanisms beyond the mere scope of language, the possibility of a common shared set of principles for domain- and modality-general sequence processing and learning was explored (Dominey 2005; Johnson et al. 2013).

2.2.2 State-of-the-art modelling approaches

The following literature review provided an overview about state-of-the-art models for the processing, learning and production of language-specific or domain-general sequences. Especially for the research question of this thesis, models that performed the learning of grammars or the extraction of statistical structure from sequential input were of particular interest. Moreover, a special focus was laid on models that implemented such skills in recurrent neural networks, with distributed encodings and purely unsupervised learning schemes. In order to compare language-specific (Tab. 2.1) and domain-general (Tab. 2.2) models, they were categorised according to their (a) architecture, (b) connectivity type, (c) encoding scheme, (d) learning mechanism and (e) learning task (Fig. 2.1):

(a) The sub-categories of the feature 'architecture' ranged from feed forward neural networks (FNNs), simple recurrent networks (SRNs), recurrent neural networks (RNNs) to reservoir computing networks (RCs). FNNs consisted of several neuronal layers that were connected unidirectionally so that the input processing occurred from input to output layers (Svozil et al. 1997; LeCun et al. 2015). SRNs were as well layered neural networks that additionally contained backward projections to earlier layers so that a complementary recurrent processing loop was achieved (Elman 1990). RNNs were single layers of neurons that reciprocally projected onto each other so that the input processing was predominantly recurrent (Douglas and Martin 2007b). RCs were combinations of a recurrently connected neural layer, i.e. the reservoir, and a readout layer (Maass et al. 2002; Lukoševičius and Jaeger 2009; Tanaka et al. 2019; Gauthier et al. 2021). Thus, the input processing occurred recurrently and feed forwardly. Finally, the sub-category 'Miscellaneous' comprised other types of neural architectures that did not fall into the previously defined sub-categories. Or further, miscellaneous models were no neural networks, for example probabilistic or Bayesian models, vector-based approaches or entropy models (Lampinen and Vehtari 2001; Kelly and West 2012).

(b) The sub-categories of the feature 'connectivity type' ranged from full, structured, random to mixed connection schemes. Full schemes were all-to-all connections of neurons. Structured schemes comprised pre-defined connectivity patterns or, in larger-scale networks, pre-defined connectivities between subareas. Random schemes had randomised neural connections that were established with pre-defined probabilities. Mixed schemes were random connectivities in combination with structured sub-networks. While structured schemes biased network dynamics, for example by supporting the convergence towards specific activity states or computations (Maass 2000), random schemes were generic and thus, implemented no specific features for the fulfilment of a certain computational task (Papadimitriou et al. 2020).

(c) The sub-categories of the feature 'encoding scheme' ranged from symbolic, continuous, binary to spiking. Further, encoding schemes of 'input' and 'processing' were distinguished. Symbolic input encodings were based on letters, digits or geometric icons. Symbolic processing schemes included algebraic manipulations of the received symbols (i.e. input letters, digits but also continuous decimal numbers of model architectures that were no neural networks). Continuous input encodings comprised time-varying signals (i.e. oscillation waves or input currents) or representations of decimal numbers that encoded the graded strength of stimulus attributes (i.e. graded feature vectors or maps).

Continuous processing schemes applied to neural networks architectures. Here, they comprised activation functions of artificial neurons (Hopfield and Tank 1986; Maass 1997) or reflected time-varying neural activities by differentiable variables (i.e. rate-based models). Binary input encodings were combinations of integer zeroes and ones where ‘one’ represented the presence and ‘zero’ the absence of a stimulus attribute or input activity. In binary processing schemes of neural networks, ‘one’ represented the spiking and ‘zero’ the silence of neurons (Hopfield 1982; Maass 1997). Finally, in spiking input encodings, stimuli were (spatio-temporal) spike trains. Spiking processing schemes were based on the discontinuous time points of neural action potential generation (Maass 1997; Izhikevich 2004). Both, binary and spiking processing schemes were considered distributed encodings.

(d) The sub-categories of the feature ‘learning mechanism’ ranged from algebraic, supervised, reinforcement learning, semi-supervised to unsupervised. Algebraic models performed learning or cognitive computations by mathematical operations (i.e. in a centralised fashion). In neural network models (i.e. distributed approaches), supervised learning (Knudsen 1994; Raymond and Medina 2018) included a teacher signal that shaped the weight changes in an error-driven process, for example by error-backpropagation (Rumelhart et al. 1986). Here, learning outcomes were judged according to a ‘right-wrong’ principle. During reinforcement learning (Kaelbling et al. 1996; Dayan and Niv 2008; Niv 2009; Arulkumaran et al. 2017; Neftci and Averbeck 2019), a reward signal shaped the weight changes whereby beneficial outputs were promoted. Thus, learning followed a goal-driven principle without the need to formulate ‘right’ or ‘wrong’ outputs (Neftci and Averbeck 2019). Semi-supervised learning was a combination of local plasticity in neural networks and the training of a readout layer via supervised or reinforcement learning. Here, both the stimulus as well as additional ‘right’, ’wrong’ or reward cues shaped the weight changes. Finally, during unsupervised learning (Barlow 1989), weight changes were purely driven by the stimulus (Doya 1999; Doya 2000) and the plasticity type implemented at synapses. Thus, learning occurred locally and in an online-fashion during the processing of the input.

(e) The sub-categories of the final feature ‘learning task’ ranged from ‘pattern or word learning’, ‘temporal structure or grammar learning’ to ‘sequence or sentence learning’. These sub-categories were motivated by the possibility that aspects of language processing and acquisition across ‘word to grammar to sentence’ levels might be explained by domain-general abilities like the learning of patterns, temporal structures or sequences. ‘Pattern or word learning’ tasks dealt with the extraction of meaningful entities from a (noisy) environment. For example, these could be visual patterns in a picture or words from the language signal. While in language the input is naturally always sequential, other domains might include temporally static patterns. Nevertheless, patterns and words were grouped into the same sub-category because of the ‘entity’-character of individual words. ‘Temporal structure or grammar learning’ tasks dealt with the sequential extraction of relevant patterns that were combinable with other entities, as for example grammatical NADs in combination with arbitrary intervening verbs. Thus, these tasks tested the ability to extract repeating or statistically significant structures from a stimulus stream. Finally, ‘sequence or sentence learning’ tasks dealt with the understanding, learning or production of complete sequences or sentences. As this capacity built up on the ability to learn and/or produce patterns or words as well as temporal structures or grammars, it was considered the most complex learning task reviewed here.

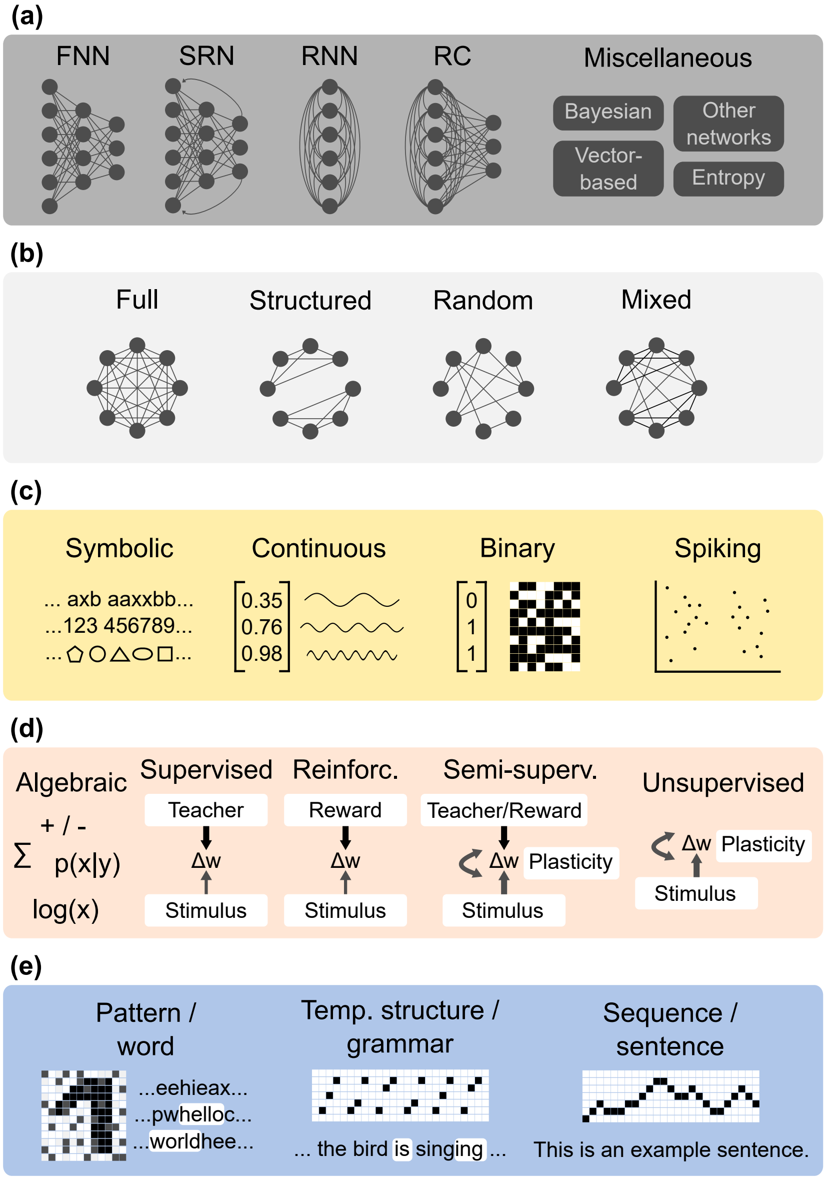


Figure 2.1: Model feature categories. (a) Architecture; FNN = feed forward network, SRN = simple recurrent network, RNN = recurrent neural network, RC = reservoir computing network. (b) Connectivity type. (c) Encoding scheme. (d) Learning mechanism; arrow widths indicate degree of contribution to weight changes (Δw). (e) Learning task.

Table 2.1: Language-specific learning models. **(a)** Architecture: miscellaneous, feed forward neural network, simple recurrent network, recurrent neural network, reservoir computing network, i.e. Misc. FNN SRN RNN RC. **(b)** Connectivity type: no connectivity, full/all-to-all, structured, random, mixed, i.e. None Full Struc. Rand. Mix.. **(c-i)** Encoding scheme of input and **(c-p)** encoding scheme of processing: symbolic, continuous, binary, spiking, i.e. Symb. Cont. Bin. Spike. **(d)** Learning mechanism: algebraic, supervised, reinforcement, semi-supervised, unsupervised, i.e. Alg. Super. Reinf. Semi. Unsu.. **(e)** Learning task: miscellaneous, 'pattern or word learning', 'temporal structure or grammar learning', 'sequence or sentence learning', i.e. Misc. P-W St-Gr Sq-Sn. Throughout: n.d. = not defined, s.n.a. = sub-categories not applicable.

Model	**a**	**b**	**c-i**	**c-p**	**d**	**e**
Hupkes et al. (2020)	Misc.	n.d.	Symb.	n.d.	Super.	Misc.
Doumas et al. (2008)	Misc.	n.d.	Symb.	Cont.	s.n.a.	
Yang and Piantadosi (2022)	Misc.	None	Symb.	Symb.	Alg.	
Heinrich and Wermter (2018)	Misc.	Rand.	Cont.	Cont.	Reinf.	
Jones and Macken (2018)	Misc.	None	Symb.	Symb.	n.d.	P-W
Perruchet and Vinter (1998)	Misc.	None	Symb.	Symb.	Alg.	
Thiessen and Pavlik Jr. (2013)	Misc.	None	Cont.	Symb.	Alg.	
Ueno et al. (2011)	Misc.	Struc.	Cont.	Cont.	Super.	
Garagnani et al. (2008)	Misc.	Struc.	Bin.	Cont.	Unsu.	
Garagnani et al. (2017)	Misc.	Struc.	n.d.	Bin.	Unsu.	
Tomasello et al. (2018)	Misc.	Struc.	Bin.	Bin.	Unsu.	
Tomasello et al. (2019)	Misc.	Struc.	Bin.	Bin.	Unsu.	
French et al. (2011)	FNN	n.d.	Symb.	Cont.	Super.	
French and Cottrell (2014)	FNN	n.d.	Symb.	Cont.	Super.	
Elman and Zipser (1988)	FNN	Full	Cont.	Cont.	Super.	
Christiansen et al. (1998)	SRN	n.d.	Cont.	Cont.	Super.	
Elman (1990)	SRN	Struc.	Bin.	Cont.	Super.	
Endress and Johnson (2021)	RNN	Full	Cont.	Cont.	Unsu.	
Fukino et al. (2016)	RC	Struc.	Cont.	Cont.	Super.	
Servan-Schreiber and Anderson (1990)	Misc.	None	Symb.	n.d.	n.d.	St-Gr
Uddén et al. (2012)	Misc.	None	Symb.	n.d.	n.d.	
Pothos (2010)	Misc.	None	Symb.	Symb.	Alg.	
Wang et al. (2019)	Misc.	None	Symb.	Symb.	Alg.	
Lieder et al. (2013)	Misc.	None	Cont.	Symb.	Alg.	
Thiessen and Pavlik Jr. (2013)	Misc.	None	Cont.	Symb.	Alg.	
Pulvermüller and Knoblauch (2009)	Misc.	Struc.	Cont.	Cont.	Unsu.	
Tong et al. (2007)	Misc.	Struc.	Bin.	Cont.	Super.	
Wacongne et al. (2012)	Misc.	Struc.	Spike	Spike	Unsu.	
Shultz and Bale (2001)	FNN	n.d.	Symb.	Cont.	Super.	
Shultz (1999)	FNN	n.d.	Cont.	Cont.	Super.	
Boucher and Dienes (2003)	FNN	n.d.	Bin.	Bin.	Alg.	
Elman and Zipser (1988)	FNN	Full	Cont.	Cont.	Super.	

Christiansen and Curtin (1999)	SRN	n.d.	n.d.	n.d.	Super.	St-Gr
Boucher and Dienes (2003)	SRN	n.d.	Cont.	n.d.	Super.	
Petersson et al. (2005)	SRN	n.d.	Cont.	Cont.	Super.	
Cleeremans and McClelland (1991)	SRN	Full	Bin.	n.d.	Super.	
Dominey and Ramus (2000)	SRN	Struc.	Cont.	Cont.	Semi.	
Fitz (2011)	RC	Rand.	Bin.	Cont.	Super.	
Duarte et al. (2014)	RC	Rand.	Bin.	Bin.	Semi.	
Weber et al. (2021)	Misc.	n.d.	Symb.	n.d.	n.d.	Sq-Sn
Goodman and Stuhlmüller (2013)	Misc.	None	Cont.	Symb.	Alg.	
Mitropolsky et al. (2021)	Misc.	Struc.	n.d.	Bin.	s.n.a	
Kriete et al. (2013)	Misc.	Struc.	Symb.	n.d.	s.n.a.	
Chang and Fitz (2014)	Misc.	Struc.	Symb.	n.d.	Super.	
Lakretz et al. (2021)	Misc.	Struc.	Symb.	Cont.	Super.	
Martin and Doumas (2017)	Misc.	Struc.	Cont.	Cont.	s.n.a.	
ten Oever and Martin (2021)	Misc.	Struc.	Cont.	Cont.	Super.	
Pitti et al. (2019)	Misc.	Struc.	Cont.	Spike	Semi.	
McClelland et al. (1989)	Misc.	Struc.	Bin.	Cont.	Super.	
Rabovsky et al. (2018)	Misc.	Struc.	Bin.	Cont.	Super.	
Fitz et al. (2020)	RNN	Rand.	Spike	Spike	s.n.a.	
Hinaut et al. (2015)	RC	Rand.	Symb.	Cont.	Super.	
Juven and Hinaut (2020)	RC	Rand.	Cont.	Cont.	Super.	
Dinh and Hinaut (2020)	RC	Rand.	Cont.	Cont.	Super.	
Hinaut and Dominey (2013)	RC	Rand.	Bin.	Cont.	Super.	

In the following, reviewed models were sorted by the increasing complexity of the learning tasks, shortly mentioning the particularly solved problem:

Misc. Miscellaneous In both language-specific and domain-general models, a fraction of studies could not be attributed to the previously defined sub-categories of learning tasks, giving rise to the 'Miscellaneous' task sub-category. In language-specific models (Tab. 2.1, see 'Misc.'), these miscellaneous tasks ranged from relational concept learning (Doumas et al. 2008), formal language acquisition (Yang and Piantadosi 2022) to the investigation of linguistic compositionality (Hupkes et al. 2020) and the implementation of embodied language acquisition in a humanoid robot (Heinrich and Wermter 2018). In domain-general models (Tab. 2.2, see 'Misc.'), miscellaneous tasks comprised the performance of goal-directed planning (Basanisi et al. 2020) and solving a bandwidth of cognitive tasks (Eliasmith 2005; Eliasmith et al. 2012; Stewart et al. 2012).

P-W Pattern or word learning 'Pattern or word learning' tasks in language-specific models (Tab. 2.1, see 'P-W') ranged from syllable recognition (Elman and Zipser 1988), pitch pattern perception (Fukino et al. 2016), phonemic category learning (Thiessen and Pavlik Jr. 2013), word prediction (Elman 1990), word chunking or segmentation (Perruchet and Vinter 1998; Christiansen et al.

1998; French et al. 2011; French and Cottrell 2014; Jones and Macken 2018; Endress and Johnson 2021) to word learning (Garagnani et al. 2008; Ueno et al. 2011; Garagnani et al. 2017; Tomasello et al. 2018; Tomasello et al. 2019). 'Pattern or word learning' tasks in domain-general models (Tab. 2.2, see 'P-W') dealt with exemplar learning and classification (Hintzman and Ludlam 1980), frequency judgements, generalisations and pair learning (Hintzman 1984), image classification (Fahlman and Lebiere 1989; Vinyals et al. 2015; Xu et al. 2015), visual chunking (Mareschal and French 2017), arbitrary pattern learning (Litwin-Kumar and Doiron 2014) and separation (Löffler and Gupta 2022) as well as the learning of written digits (Brader et al. 2007; Diehl and Cook 2015; Panda et al. 2018), spoken digits (Klampfl and Maass 2013) and geometric shapes (Zenke et al. 2015).

St-Gr **Temporal structure or grammar learning** 'Temporal structure or grammar learning' tasks in language-specific models (Tab. 2.1, see 'St-Gr') ranged from feature learning from continuous speech (Elman and Zipser 1988), serial structure learning (Dominey and Ramus 2000; Tong et al. 2007), grammatical rule learning (Cleeremans and McClelland 1991; Christiansen and Curtin 1999; Shultz 1999; Shultz and Bale 2001; Petersson et al. 2005; Pulvermüller and Knoblauch 2009; Pothos 2010; Duarte et al. 2014), adjacent dependency learning (Servan-Schreiber and Anderson 1990; Boucher and Dienes 2003) to non-adjacent dependency acquisition (Fitz 2011; Uddén et al. 2012; Thiessen and Pavlik Jr. 2013; Wang et al. 2019) and mismatch negativity production during oddball training (Wacongne et al. 2012; Lieder et al. 2013). 'Temporal structure or grammar learning' tasks in domain-general models (Tab. 2.2, see 'St-Gr') ranged from structure learning in sequential stimulus streams (Lazar et al. 2009; Lazar et al. 2011; Toutounji and Pipa 2014; Aswolinskiy and Pipa 2015; Hartmann et al. 2015; Cui et al. 2016) to pattern onset detection (Masquelier et al. 2008) and sequence chunking (Fonollosa et al. 2015).

Sq-Sn **Sequence or sentence learning** 'Sequence or sentence learning' tasks in language-specific models (Tab. 2.1, see 'Sq-Sn') ranged from oscillation-based tracking of hierarchical linguistic structure (Martin and Doumas 2017) and speech (ten Oever and Martin 2021), speech perception and production (Pitti et al. 2019), sentence processing (Fitz et al. 2020), sentence parsing (Mitropolsky et al. 2021), sentence comprehension (McClelland et al. 1989; Hinaut and Dominey 2013; Kriete et al. 2013; Rabovsky et al. 2018; Juven and Hinaut 2020; Dinh and Hinaut 2020), sentence production (Chang and Fitz 2014; Hinaut et al. 2015) to nested dependency learning in sentences (Lakretz et al. 2021), parsing of negative polarity items (Weber et al. 2021) and language understanding in social situations (Goodman and Stuhlmüller 2013). 'Sequence or sentence learning' tasks in domain-general models (Tab. 2.2, see 'Sq-Sn') ranged from the generation of pre-movement signals (Sussillo and Abbott 2009), sensorimotor control tasks (Tetzlaff et al. 2015; Rueckert et al. 2016; Enel et al. 2016; Rapp and Nawrot 2020), time series classification (Aswolinskiy et al. 2018), sequence processing (Duarte and Morrison 2014;

Setareh et al. 2018), sequence learning (Hoerzer et al. 2014; Liang et al. 2020; Klos et al. 2020; Maes et al. 2020; Vincent-Lamarre et al. 2020; Maes et al. 2021), sequence recall or replay (Dominey et al. 1995; Fonollosa et al. 2015; Tully et al. 2016; Fiebig and Lansner 2017; Klos et al. 2018; Martinez et al. 2019; Löffler and Gupta 2020) to sequence production (Panda and Roy 2017; Cazin et al. 2019; Fang et al. 2021).

Table 2.2: Domain-general learning models. **(a)** Architecture: miscellaneous, feed forward neural network, simple recurrent network, recurrent neural network, reservoir computing network, i.e. Misc. FNN SRN RNN RC. **(b)** Connectivity type: no connectivity, full/all-to-all, structured, random, mixed, i.e. None Full Struc. Rand. Mix.. **(c-i)** Encoding scheme of input and **(c-p)** encoding scheme of processing: symbolic, continuous, binary, spiking, i.e. Symb. Cont. Bin. Spike. **(d)** Learning mechanism: algebraic, supervised, reinforcement, semi-supervised, unsupervised, i.e. Alg. Super. Reinf. Semi. Unsu.. **(e)** Learning task: miscellaneous, 'pattern or word learning', 'temporal structure or grammar learning', 'sequence or sentence learning', i.e. Misc. P-W St-Gr Sq-Sn. Throughout: n.d. = not defined, s.n.a. = sub-categories not applicable.

Model	**a**	**b**	**c-i**	**c-p**	**d**	**e**
Eliasmith (2005)	Misc.	Struc.	Cont.	Spike	s.n.a.	Misc.
Basanisi et al. (2020)	Misc.	Struc.	Bin.	Bin.	Semi.	
Eliasmith et al. (2012)	Misc.	Struc.	Spike	Spike	s.n.a.	
Stewart et al. (2012)	Misc.	Struc.	Spike	Spike	s.n.a.	
Hintzman (1984)	Misc.	None	Symb.	Symb.	Alg.	P-W
Hintzman and Ludlam (1980)	Misc.	None	Cont.	Symb.	Alg.	
Vinyals et al. (2015)	Misc.	Struc.	Cont.	Cont.	Super.	
Xu et al. (2015)	Misc.	Struc.	Cont.	Cont.	Super.	
Brader et al. (2007)	Misc.	Struc.	Spike	Spike	Semi.	
Diehl and Cook (2015)	Misc.	Struc.	Spike	Spike	Unsu.	
Löffler and Gupta (2022)	Misc.	Mix.	Spike	Spike	s.n.a	
Mareschal and French (2017)	FNN	n.d.	n.d.	Cont.	Super.	
Fahlman and Lebiere (1989)	FNN	Full	Symb.	Cont.	Super.	
Panda et al. (2018)	FNN	Full	Spike	Spike	Unsu.	
Zenke et al. (2015)	RNN	Rand.	Spike	Spike	Unsu.	
Litwin-Kumar and Doiron (2014)	RNN	Rand.	Spike	Spike	Unsu.	
Klampfl and Maass (2013)	RC	Mix.	Spike	Spike	Semi.	
Fonollosa et al. (2015)	Misc.	Struc.	Bin.	Cont.	Unsu.	St-Gr
Cui et al. (2016)	Misc.	Struc.	Bin.	Bin.	Unsu.	
Masquelier et al. (2008)	Misc.	Struc.	Spike	Spike	Unsu.	
Lazar et al. (2009)	RC	Rand.	Bin.	Bin.	Semi.	
Lazar et al. (2011)	RC	Rand.	Bin.	Bin.	Semi.	
Toutounji and Pipa (2014)	RC	Rand.	Bin.	Bin.	Semi.	
Aswolinskiy and Pipa (2015)	RC	Rand.	Bin.	Bin.	Semi.	
Hartmann et al. (2015)	RC	Rand.	Bin.	Bin.	Semi.	

Dominey et al. (1995)	Misc.	Struc.	Cont.	Cont.	Reinf.	Sq-Sn
Martinez et al. (2019)	Misc.	Struc.	Cont.	Cont.	Unsu.	
Rapp and Nawrot (2020)	Misc.	Struc.	Cont.	Spike	Reinf.	
Liang et al. (2020)	Misc.	Struc.	Cont.	Spike	Semi.	
Fang et al. (2021)	Misc.	Struc.	Cont.	Spike	Semi.	
Fonollosa et al. (2015)	Misc.	Struc.	Bin.	Cont.	Unsu.	
Maes et al. (2021)	Misc.	Struc.	Spike	Spike	Semi.	
Löffler and Gupta (2020)	Misc.	Struc.	Spike	Spike	Unsu.	
Tully et al. (2016)	Misc.	Struc.	Spike	Spike	Unsu.	
Fiebig and Lansner (2017)	Misc.	Struc.	Spike	Spike	Unsu.	
Setareh et al. (2018)	Misc.	Struc.	Spike	Spike	Unsu.	
Panda and Roy (2017)	RNN	Rand.	Spike	Spike	Unsu.	
Klos et al. (2018)	RNN	Mix.	Spike	Spike	Unsu.	
Sussillo and Abbott (2009)	RC	Rand.	Cont.	Cont.	Super.	
Enel et al. (2016)	RC	Rand.	Cont.	Cont.	Super.	
Cazin et al. (2019)	RC	Rand.	Cont.	Cont.	Super.	
Aswolinskiy et al. (2018)	RC	Rand.	Cont.	Cont.	Super.	
Klos et al. (2020)	RC	Rand.	Cont.	Cont.	Super.	
Hoerzer et al. (2014)	RC	Rand.	Cont.	Cont.	Reinf.	
Tetzlaff et al. (2015)	RC	Rand.	Cont.	Cont.	Semi.	
Vincent-Lamarre et al. (2020)	RC	Rand.	Cont.	Spike	Super.	
Rueckert et al. (2016)	RC	Rand.	Bin.	Bin.	Reinf.	
Duarte and Morrison (2014)	RC	Rand.	Spike	Spike	Semi.	
Maes et al. (2020)	RC	Mix.	Spike	Spike	Semi.	

In this collection of state-of-the art sequence learning models, the class of interest for this thesis (i.e. single layers of randomly connected recurrent neural networks) was strongly underrepresented. Only a small fraction of studies used exclusively simple RNNs as a modelling substrate (Litwin-Kumar and Doiron 2014; Zenke et al. 2015; Panda and Roy 2017; Klos et al. 2018; Fitz et al. 2020; Endress and Johnson 2021). The majority of remaining neural networks either implemented specifically structured architectures (i.e. miscellaneous networks), FNNs, SRNs or RCs. However, specifically structured network models incorporated recurrent network modules throughout (Dominey et al. 1995; Garagnani et al. 2008; Pulvermüller and Knoblauch 2009; Wacongne et al. 2012; Fonollosa et al. 2015; Vinyals et al. 2015; Xu et al. 2015; Tully et al. 2016; Fiebig and Lansner 2017; Garagnani et al. 2017; Tomasello et al. 2018; Heinrich and Wermter 2018; Setareh et al. 2018; Tomasello et al. 2019; Pitti et al. 2019; Martinez et al. 2019; Basanisi et al. 2020; Liang et al. 2020; Lakretz et al. 2021; Maes et al. 2021; Mitropolsky et al. 2021; ten Oever and Martin 2021). Further, also RC models relied on a recurrent reservoir as an essential network component (Lazar et al. 2009; Sussillo and Abbott 2009; Lazar et al. 2011; Fitz 2011; Klampfl and Maass 2013; Hinaut and Dominey 2013; Duarte et al. 2014; Duarte and Morrison 2014; Hoerzer et al. 2014; Toutounji and Pipa 2014; Tetzlaff et al. 2015; Aswolinskiy and Pipa 2015; Hartmann et al. 2015; Hinaut et al. 2015; Fukino et al. 2016; Rueckert et al. 2016; Enel et al. 2016; Aswolinskiy et al. 2018; Cazin et al. 2019; Klos et al. 2020; Juven and Hinaut 2020; Dinh and Hinaut 2020; Vincent-Lamarre et al. 2020; Maes et al. 2020). Therefore, generic recurrent network modules can be seen as important features amongst other, more specific architectural structures (Dominey 2013). However, combinations of different module types inevitably lead to the difficulty of disentangling their individual contributions to the learning outcome. For example, are RC models successful sequence learners because of the recurrent reservoir or because of the supervised training of the readout layer? Here, increased RC learning performances by plastic instead of static reservoirs already highlighted the importance of learning in the recurrent layer (Lazar et al. 2009; Toutounji and Pipa 2014). This thesis therefore further investigated the idea that an essential proportion of the learning capacity might already be implemented in generic recurrent layers of neurons, i.e. in a small-scale recurrent building block of cortex without any further architectural pre-definitions. Next to architecture, the reviewed collection of language-specific models further revealed an underrepresentation of both distributed, i.e. binary or spiking, processing schemes and unsupervised learning. Throughout, a fraction of models was based on symbolic processing schemes that went together with algebraic implementations of learning (Perruchet and Vinter 1998; Pothos 2010; Goodman and Stuhlmüller 2013; Lieder et al. 2013; Thiessen and Pavlik Jr. 2013; Wang et al. 2019; Yang and Piantadosi 2022). Among distributed networks, semi-supervised learning (Duarte et al. 2014; Pitti et al. 2019) and fully unsupervised learning were occasionally applied (Wacongne et al. 2012; Garagnani et al. 2017; Tomasello et al. 2018; Tomasello et al. 2019). Even though neural networks in the form of FNNs, SRNs and RCs were widely implemented, their predominantly continuous processing schemes were primarily combined with semi- or fully supervised learning (Elman and Zipser 1988; Christiansen et al. 1998; Elman 1990; Shultz 1999; Shultz and Bale 2001; Dominey and Ramus 2000; Petersson et al. 2005; Fitz 2011; French et al. 2011; Hinaut and Dominey 2013; Hinaut et al. 2015; French and Cottrell 2014; Fukino et al. 2016; Juven and Hinaut 2020; Dinh and Hinaut 2020). Thus, the question how unsupervised, associative learning of language might be implemented in the brain remained largely unaddressed by theses state-of-the-art language learning models. On the contrary, in domain-general learning models, binary or spiking processing schemes were commonly applied and often endowed with unsupervised learning (Masquelier et al. 2008; Litwin-Kumar and Doiron 2014; Diehl and Cook 2015; Zenke et al. 2015; Cui et al. 2016; Tully et al. 2016; Fiebig and Lansner 2017; Panda and Roy 2017; Klos et al. 2018; Setareh et al. 2018; Panda et al. 2018; Löffler and Gupta 2020). Fully supervised learning mechanisms were again primarily implemented in neural networks that were based on continuous processing schemes (Fahlman and Lebiere 1989; Sussillo and Abbott 2009; Vinyals et al. 2015; Xu et al. 2015; Enel et al. 2016; Mareschal and French 2017; Aswolinskiy et al. 2018; Cazin et al. 2019; Klos et al. 2020). Taken together and throughout, unsupervised learning was mainly applied in distributed networks. Distributed and unsupervised domain-general models further had a wide applicability in sequence learning problems across the defined task categories. However, distributed networks remained underrepresented in language-specific sequence learning problems. Thus, their potential to model aspects of unsupervised language acquisition has to a large extent not been explored yet.

2.2.3 Unsupervised grammar learning models are rare

A closer look at language-specific neural network models in the 'temporal structure or grammar learning' task category revealed only two studies that applied fully unsupervised learning mechanisms (Pulvermüller and Knoblauch 2009; Wacongne et al. 2012). As of special interest to this thesis, their implementation of unsupervised learning was 'Hebbian' (Pulvermüller and Knoblauch 2009) or even based on spike-timing dependent plasticity (Wacongne et al. 2012). However, in the 'pattern or word learning' task category, some more unsupervised neural network approaches existed. Here, 'Hebbian' learning found application in a small scale recurrent network (Endress and Johnson 2021) and in more detailed cortical networks (Garagnani et al. 2008; Garagnani et al. 2017; Tomasello et al. 2018; Tomasello et al. 2019). In the most complex 'sequence or sentence learning' task category, however, no unsupervised learning models could be identified. Taken together, even though not widely applied yet, the identified unsupervised models provided important first hints towards a general applicability of unsupervised learning in neural networks for language-specific problems. Further, some symbolic or algebraic models implemented statistical learning with principles resembling unsupervised learning schemes. For example, the frequency effect of repeatedly co-occurring stimulus elements played a central role in a vector-based chunking model (Perruchet and Vinter 1998). But also principles of long-term memory like stimulus activation and decay were implemented as underlying mechanisms of learning (Thiessen and Pavlik Jr. 2013). Interestingly for this thesis, the effect of variability on NAD acquisition has been investigated already to some extent. Here, a beneficial effect of large variabilities in the intervening material has been demonstrated in a vector-based model of statistical learning (Thiessen and Pavlik Jr. 2013). Further, a liquid state machine model reproduced human performance curves across variability conditions (Fitz 2011). Thus, similar NAD benchmark variations like those identified for this thesis (Wilson et al. 2018) have already been applied for testing the performance of other language learning model classes. Taken together, some modelling approaches for the unsupervised acquisition of statistical structure and human language learning performances existed (Frank et al. 2010; Perruchet and Tillmann 2010; Rohrmeier and Cross 2014). However, the model review revealed that neurobiologically motivated approaches primarily dealt with other learning problems than grammar acquisition, as for example word learning (Garagnani et al. 2008; Garagnani et al. 2017; Tomasello et al. 2018; Tomasello et al. 2019). Models that dealt with the specific problem of NAD acquisition were, however, either vector-based (Thiessen and Pavlik Jr. 2013) or supervised (Fitz 2011). Therefore, neurobiologically motivated (i.e. distributed) networks for the unsupervised acquisition of non-adjacent grammars have not been studied to a satisfactory degree yet. This thesis therefore further aimed at filling this gap and at extending existing lines of (statistical) grammar learning modelling research (Chang et al. 2012; Zuidema et al. 2020).

Chapter 3

Modelling the spike-based acquisition of grammars

3.1 Grammar learning experiments

3.1.1 Preliminary remarks

The manuscript ‘Spike-based statistical learning explains human grammar acquisition performance’ contains the main materials and results of this thesis about modelling the spike-based acquisition of grammatical structure in form of isolated or nested non-adjacent dependencies (NADs) with a spiking recurrent neural network. The manuscript, from now on referred to as Lehfeldt et al. (n.d.), shows a selection of learning performance measures (i.e. so called separability measures) and the respectively underlying synapse parameters (i.e. synaptic weights). These demonstrated an accordance between modelled and human grammar acquisition performance patterns. The supplementary material of Lehfeldt et al. (n.d.) further contains the full collection of underlying synapse assembly weights and the grammatical training sequence statistics of all experiments and across all recurrent networks tested. Additional material for demonstrating basic dynamics of the model and further result data from the grammar learning experiments are presented in this thesis under ‘Model demonstration’ (see Sec. 3.2) and ‘Grammar learning experiments: additional material’ (see Sec. 3.3).

3.1.2 Manuscript and supplementary material

After thesis submission, a peer-reviewed version of the manuscript ‘Spike-based statistical learning explains human grammar acquisition performance’ (Lehfeldt et al. n.d.) has been published:

Lehfeldt, S., Mueller, J. L., and Pipa, G. (2022). “Spike-based statistical learning explains human performance in non-adjacent dependency learning tasks”. In: *Frontiers in Cognition* 1, 1026819. DOI: 10.3389/fcogn.2022.1026819.

This thesis contains numerous references to the original version of the manuscript. For reviewing the referenced content, please refer to the above mentioned publication.

3.2 Model demonstration

3.2.1 Spiking neural network simulator

The simulations of this thesis were conducted in Python using the 'Brian2' spiking neural network simulator (Stimberg et al. 2014; Stimberg et al. 2019). This is the follow-up version of the original 'Brian' simulator (Goodman and Brette 2008; Goodman and Brette 2009). 'Brian2' uses a mathematical string notation format for the definition of neuron and synapse models, whereby continuously evolving state variables are described by differential equations in combination with spike-triggered update routines (Stimberg et al. 2014). In the following, neuron and synapse models of the RNN were therefore presented by demonstrating their state variable and spike-triggered update dynamics during the online-processing of external spiking input. Throughout, simulations were conducted with a time step resolution of 0.1 ms. Neuron and synapse model equations were solved using the 'euler' method.

3.2.2 RNN connectivity

The network architecture of the recurrent neural network (RNN) model was described in detail in Sec. 3.1.2, 'Network architecture' (Lehfeldt et al. n.d.). Here, the synaptic connectivity of an example RNN was shown for demonstrating the randomised projections within and between the excitatory (E) and inhibitory (I) population as well as the one-to-one connection scheme between the input and excitatory neurons (Fig. 3.9).

3.2.3 Neuron model dynamics

3.2.3.1 LIF neuron

Leaky integrate-and-fire (LIF) neuron models of the RNN were derived from the LIF-SORN by Miner and Triesch (2016) and comprised the following set of variables and parameters: a membrane voltage (V_m), a membrane voltage time constant (τ_{V_m}), a resting voltage ($V_{\hookrightarrow}$), a reset voltage ($V_{\perp}$) and a threshold voltage for spiking (V_θ). While the activity state of a LIF neuron was modelled by the state variable V_m, the parameters τ_{V_m}, $V_{\hookrightarrow}$, $V_{\perp}$ and V_θ represented the parameter space within which LIF neuron dynamics evolved. Here, neuron model dynamics were demonstrated in small scale networks where an excitatory or inhibitory LIF neuron with a fixed V_θ received a Poisson spike train as input (Fig. 3.10). For a description of the LIF neuron model, see equations (3.1a) to (3.1c) in Sec. 3.1.2 'Leaky integrate-and-fire neurons (LIF) with intrinsic plasticity (IP)' (Lehfeldt et al. n.d.). Each input spike to a LIF neuron caused an increase of the neuron's V_m by the voltage value of the connecting synapse. For details, see equation (3.3) in Sec. 3.1.2 'Synaptic transmission' (Lehfeldt et al. n.d.). In the absence of input spikes V_m decayed, i.e. leaked, back to $V_{\hookrightarrow}$. However, under a repeated input activation, V_m integrated the received input spikes in an accumulative way. Thus, once it's value crossed V_θ, the emission of a spike was triggered. After the emission of a spike, V_m was reset to $V_{\perp}$ and a new input integration cycle started.

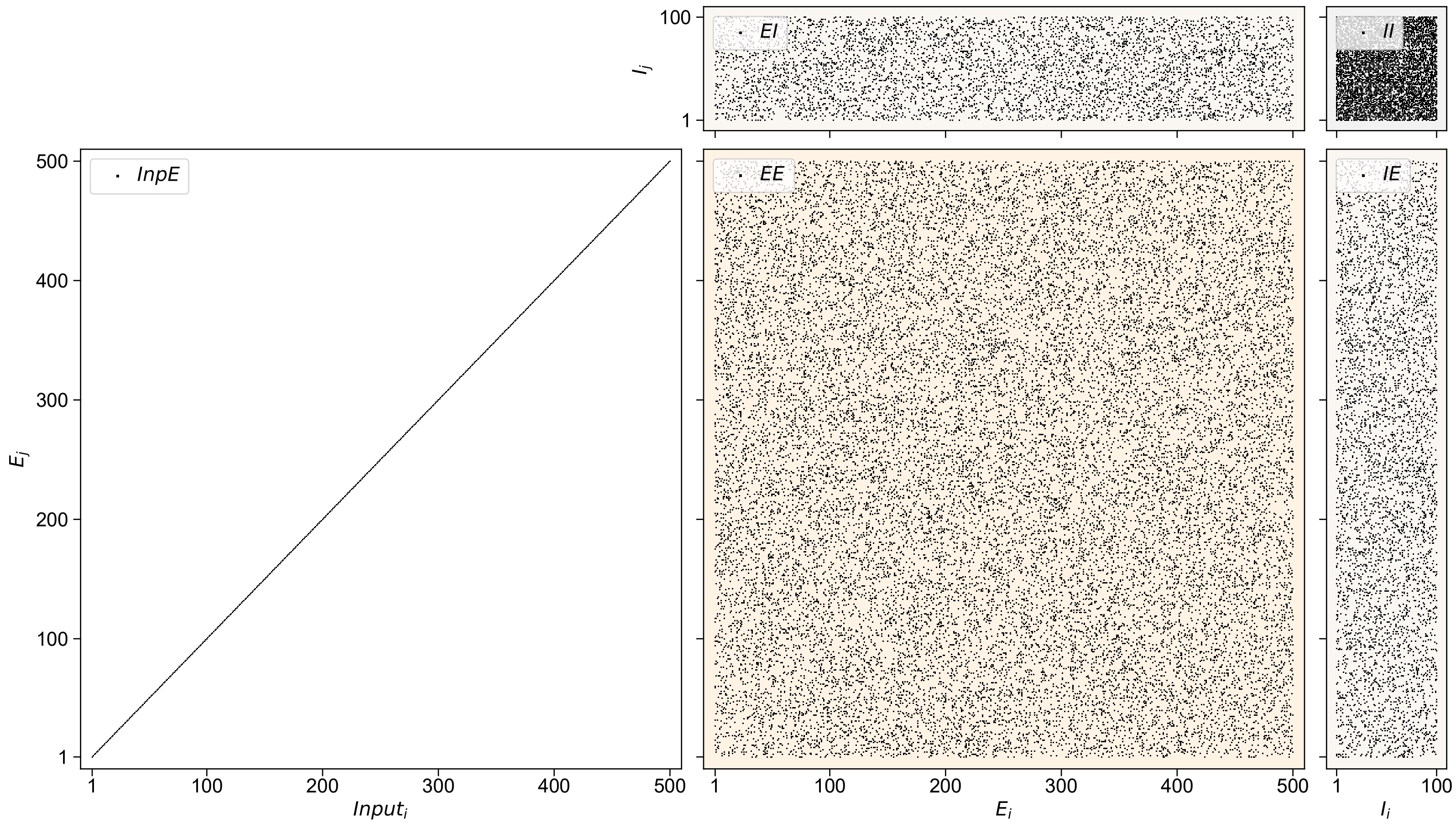


Figure 3.9: Connectivity of an example RNN from the grammar learning experiment series. Each dot represents a synaptic connection between a presynaptic (i) and postsynaptic (j) neuron. Synaptic connections ($p =$ connection probability): $InpE$ = input-to-excitatory (one-to-one connection scheme), EE = excitatory-to-excitatory ($p_{EE} = 0.1$), EI = excitatory-to-inhibitory ($p_{EI} = 0.1$), IE = inhibitory-to-excitatory ($p_{IE} = 0.1$), II = inhibitory-to-inhibitory ($p_{II} = 0.5$).

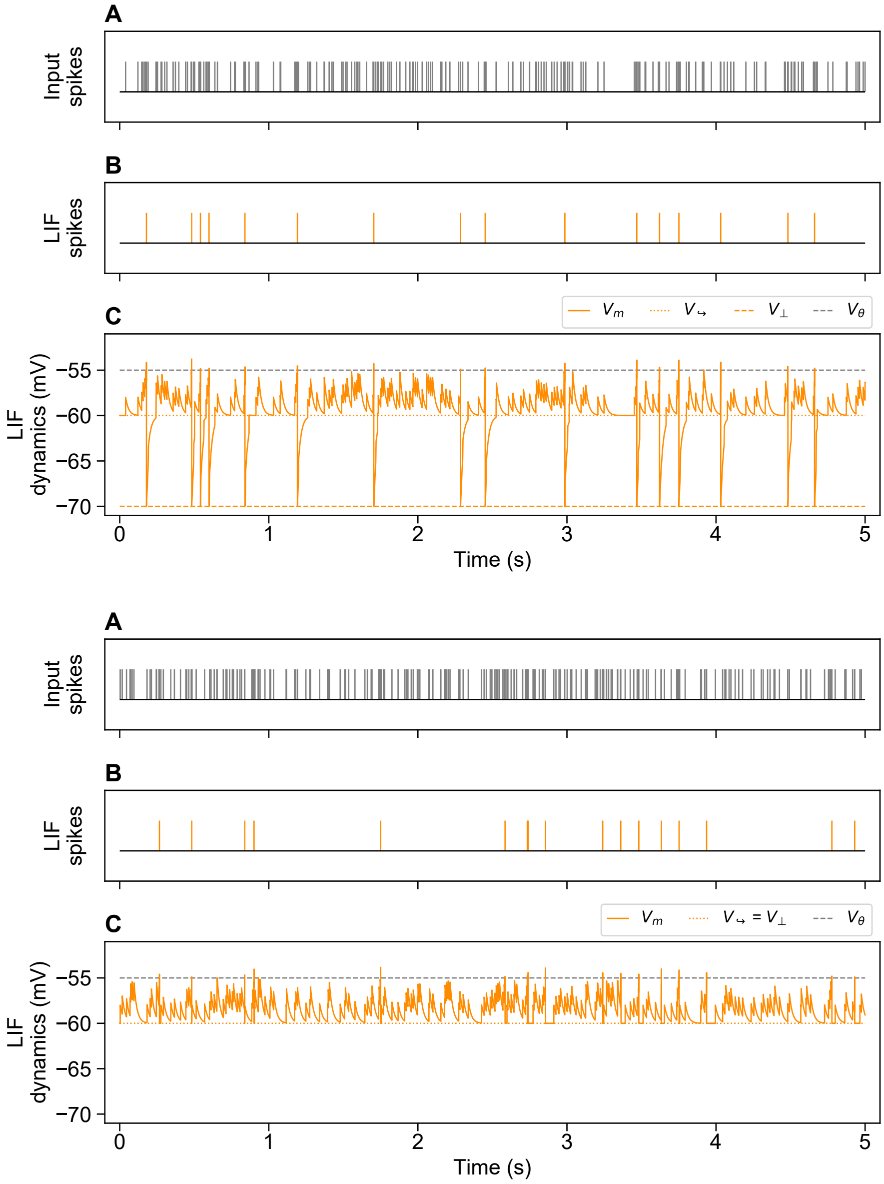


Figure 3.10: LIF neuron dynamics with fixed threshold for spiking. Excitatory (**top**) and inhibitory (**bottom**) LIF neuron. **A** Poisson input spikes. **B** LIF neuron output spikes. **C** LIF neuron variables; V_m = membrane voltage; $V_{\hookrightarrow}$ = resting voltage; $V_{\perp}$ = reset voltage; V_{θ} = threshold voltage. Neuron parameter space as in Lehfeldt et al. (n.d.).

3.2.3.2 LIF neuron with IP

As in the SORN (Lazar et al. 2009) and LIF-SORN (Miner and Triesch 2016), LIF neurons further comprised an intrinsic plasticity (IP) of V_{θ}. Here, the implementation of IP was derived from Stimberg et al. (2014). For a description of the IP model, see equations (3.2a) and (3.2b) in Sec. 3.1.2 'Leaky integrate-and-fire neurons (LIF) with intrinsic plasticity (IP)' (Lehfeldt et al. n.d.). The IP model converted V_{θ} into a neuronal state variable and introduced three additional parameters: a threshold

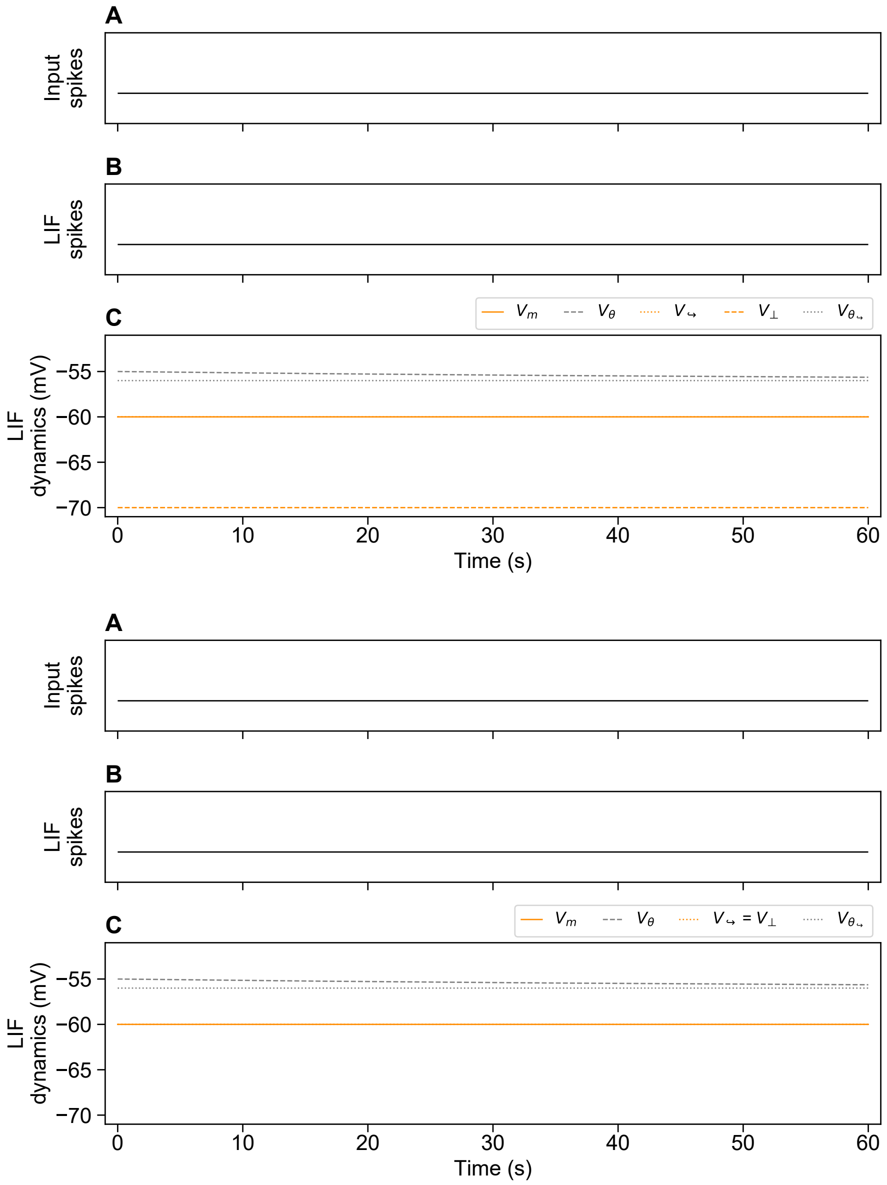


Figure 3.11: IP dynamics in the absence of LIF neuron spiking activity. Excitatory (**top**) and inhibitory (**bottom**) LIF neuron. **A** No input spikes. **B** No LIF neuron output spikes. **C** LIF neuron variables; V_m = membrane voltage; V_θ = threshold voltage; $V_\hookrightarrow$ = resting voltage; $V_\perp$ = reset voltage; $V_{\theta_\hookrightarrow}$ = threshold resting voltage. Neuron parameter space as in Lehfeldt et al. (n.d.).

resting voltage ($V_{\theta_\hookrightarrow}$), a threshold voltage time constant (τ_{V_θ}) and a threshold voltage increase (V_{θ_Δ}). Thus, instead of being fixed at a constant value, V_θ decayed to $V_{\theta_\hookrightarrow}$ in the absence of LIF neuron spiking activity (Fig. 3.11). After the emission of a LIF neuron spike, V_θ was increased by V_{θ_Δ}. Therefore, V_θ successively increased during a repeated emission of spikes that occurred within the temporal window of the V_θ decay as defined by τ_{V_θ} (Fig. 3.12).

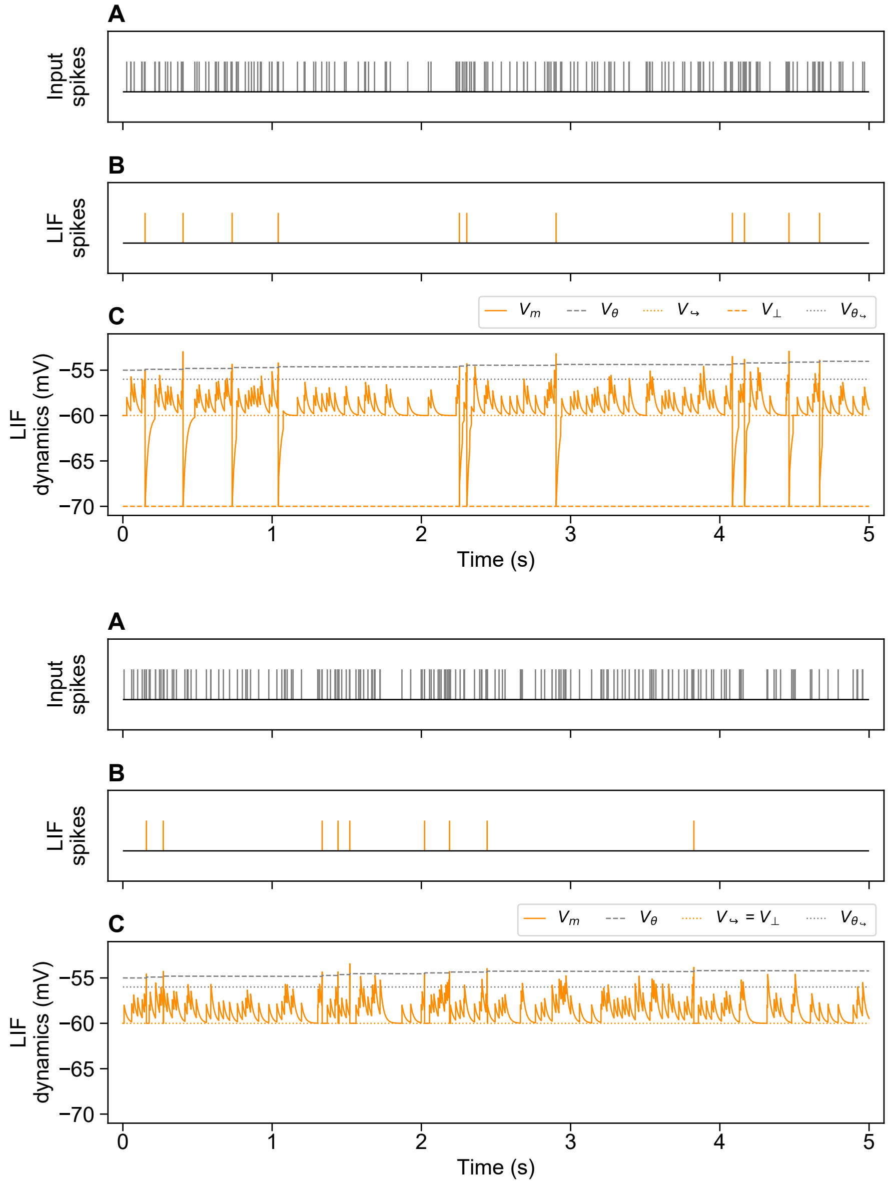


Figure 3.12: LIF neuron dynamics with IP. Excitatory (**top**) and inhibitory (**bottom**) LIF neuron. **A** Poisson input spikes. **B** LIF neuron output spikes. **C** LIF neuron variables; V_m = membrane voltage; V_θ = threshold voltage; $V_\hookrightarrow$ = resting voltage; $V_\perp$ = reset voltage; $V_{\theta_\hookrightarrow}$ = threshold resting voltage. Neuron parameter space as in Lehfeldt et al. (n.d.).

3.2.4 Synapse model dynamics

3.2.4.1 STDP synapse

As in the SORN (Lazar et al. 2009) and LIF-SORN (Miner and Triesch 2016), learning occurred in plastic excitatory-to-excitatory (EE) synapses of the RNN. Here, spike-timing dependent plasticity (STDP) was combined with a short- to long-term memory transition (SLMT) mechanism that was developed in this thesis. Before introducing SLMT, the dynamics of a STDP synapse were demonstrated in a small

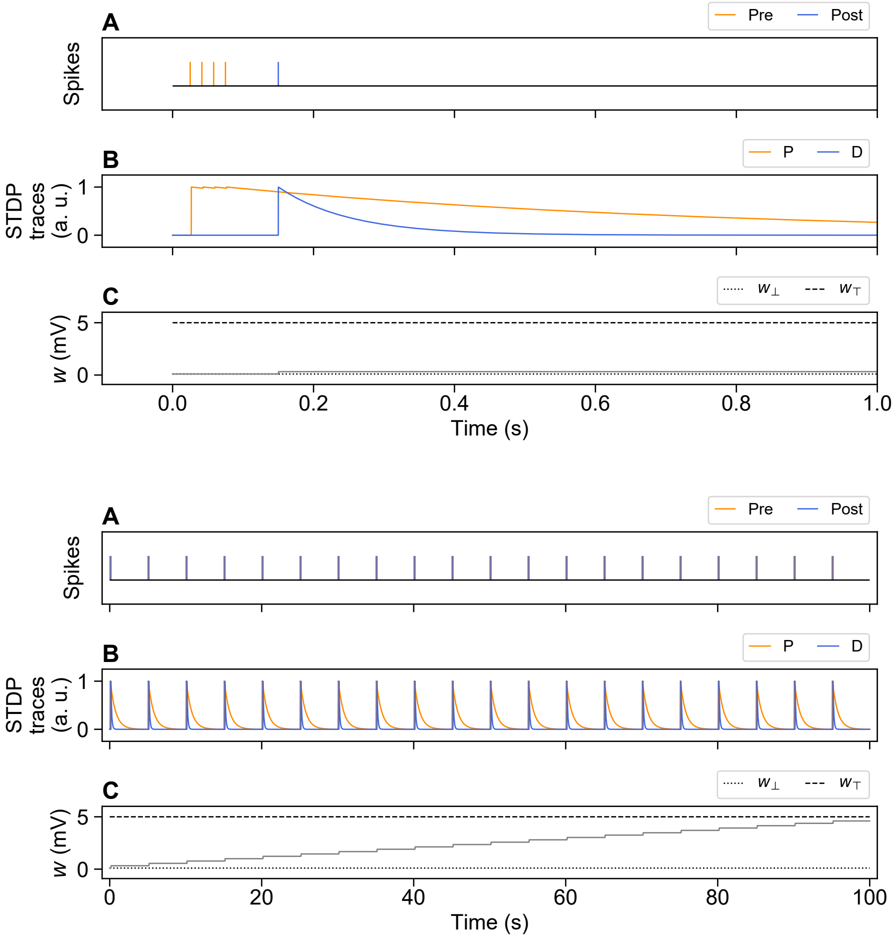


Figure 3.13: STDP synapse experiencing a series of *pre-post* spike pairings. Zoom into the first second (**top**) and full simulation run (**bottom**). **A** Spikes at the synapse; Pre = presynaptic spikes; Post = postsynaptic spikes. **B** STDP traces; P = potentiation trace; D = depression trace. **C** Synaptic weight; $w_\perp$ = lower weight boundary; $w_\top$ = upper weight boundary. Synapse parameter space as in Lehfeldt et al. (n.d.).

scale network with single pre- and postsynaptic neurons that were connected by a single plastic synapse (Fig. 3.13 and Fig. 3.14). For a description of the STDP synapse model, see equations (3.4a) to (3.4c) in Sec. 3.1.2 'Spike-timing dependent plasticity (STDP) with short- to long-term memory transition (SLMT)' (Lehfeldt et al. n.d.). A plastic STDP synapse was described by three state variables: a synaptic weight (w), a potentiation trace (P) and a depression trace (D). Further, the parameter space comprised a lower ($w_\perp$) and upper ($w_\top$) weight boundary, a potentiation trace time constant (τ_P), a depression trace time constant (τ_D), a weight potentiation maximum ($P_{\top w}$), a weight depression maximum ($D_{\perp w}$) and a trace maximum ($T_\top$). The temporal correlation of pre- and postsynaptic spikes at the synapse triggered weight changes by the following update routines. While the occurrence of presynaptic spikes elicited a maximisation of P, the occurrence of postsynaptic spikes elicited a maximisation of D. In the absence of pre- or postsynaptic

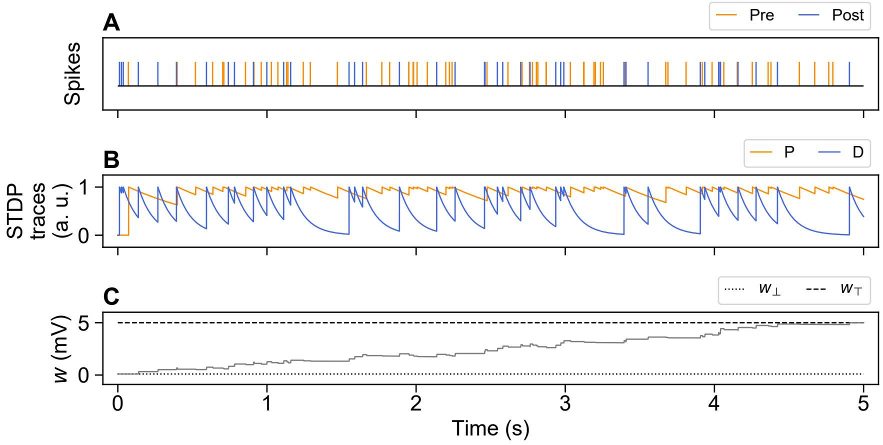


Figure 3.14: STDP synapse experiencing a Poisson pre- and postsynaptic input. **A** Spikes at the synapse; Pre = presynaptic spikes; Post = postsynaptic spikes. **B** STDP traces; P = potentiation trace; D = depression trace. **C** Synaptic weight; $w_\perp$ = lower weight boundary; $w_\top$ = upper weight boundary. Synapse parameter space as in Lehfeldt et al. (n.d.).

spikes at the synapse, both P and D decayed back to zero within temporal windows defined by τ_P and τ_D, respectively. After a *pre-post* spike pairing, i.e. after the occurrence of a postsynaptic spike, w was increased by the potentiation maximum value $P_{\top_w}$ that was scaled by the current value of P. Equivalently, after a *post-pre* spike pairing, i.e. after the occurrence of a presynaptic spike, w was decreased by the depression maximum value $D_{\perp_w}$ that was scaled by the current value of D. Thus, while positively correlated spike pairings induced potentiation, negatively correlated spike pairings induced depression. Further, larger weight changes were induced for temporally close spike pairings while smaller weight changes occurred for temporally distant spike pairings. Figure 3.13 demonstrated a constantly growing w at a STDP synapse that experienced a series of *pre-post* spike pairings. Figure 3.14 demonstrated the dynamics of w during a Poisson pre- and postsynaptic input where both *pre-post* and *post-pre* spike pairings occurred concurrently and thus, also both potentiation and depression. However, as STDP was skewed towards potentiation by $\tau_P > \tau_D$ and $P_{\top_w} > D_{\perp_w}$, w gradually grew towards $w_\top$.

3.2.4.2 STDP synapse with SLMT

The STDP synapse model was extended by a short- to long-term memory transition (SLMT) mechanism that introduced a decay of w with a plastic weight time constant (τ_w). The SLMT mechanism developed in this thesis bears similarity to the 'adaptive synaptic plasticity (ASP)' mechanism (Panda and Roy 2017; Panda et al. 2018) as both included a weight decay with adaptive τ_w. However, SLMT was symmetric and its plasticity fully based on the STDP traces. For a full description of the SLMT model, see equations (3.5a) to (3.5c) in Sec. 3.1.2 'Spike-timing dependent plasticity (STDP) with short- to long-term memory transition (SLMT)' (Lehfeldt et al. n.d.). A STDP synapse with SLMT included the plastic τ_w as an additional synaptic state

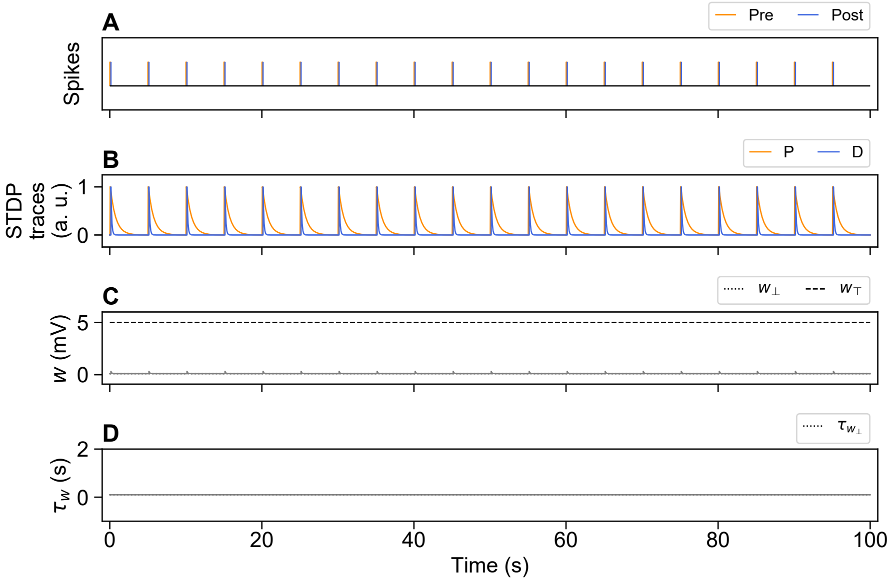


Figure 3.15: STDP synapse with SLMT experiencing a series of *pre-post* spike pairings while τ_w was non-plastic and short. **A** Spikes at the synapse; Pre = presynaptic spikes; Post = postsynaptic spikes. **B** STDP traces; P = potentiation trace; D = depression trace. **C** Synaptic weight; $w_\perp$ = lower weight boundary; $w_\top$ = upper weight boundary. **D** Synaptic weight time constant; $\tau_{w_\perp}$ = lower weight time constant boundary. Synapse parameter space as in Lehfeldt et al. (n.d.), except for $D_{\perp\tau_w} = 0$ s and $P_{\top\tau_w} = 0$ s.

variable. Further, the synaptic parameter space was extended by a resting weight ($w_\perp$), a weight time constant potentiation maximum ($P_{\top\tau_w}$), a weight time constant depression maximum ($D_{\perp\tau_w}$) and a lower ($\tau_{w_\perp}$) and upper ($\tau_{w_\top}$) weight time constant boundary. Weight time constant changes followed the same spike-triggered update routines as w in STDP. Thus, after the occurrence of a postsynaptic spike at the synapse, τ_w was potentiated, i.e. increased by the potentiation maximum $P_{\top\tau_w}$ that was scaled by the current value of P. Equivalently, after the occurrence of a presynaptic spike, τ_w was decreased by the depression maximum value $D_{\perp\tau_w}$ that was scaled by the current value of D. In the following, the dynamics of a STDP synapse with SLMT were demonstrated again in a small scale network with single pre- and postsynaptic neurons that were connected by a single plastic synapse (Fig. 3.15, Fig. 3.16, Fig. 3.17, Fig. 3.18 and Fig. 3.19). Figure 3.15 demonstrated the dynamics of w with a non-plastic and short τ_w during the repeated experience of *pre-post* spike pairings. As τ_w was short and remained constant at its initialisation value, plasticity-induced weight changes were not permanent and w decayed quickly back to $w_\perp$. Thus, despite a repeated experience of *pre-post* spike pairings, the synaptic weight did not grow on a temporally consistent scale. Figure 3.16 demonstrated how the growth of w with a plastic τ_w became possible under a repeated experience of *pre-post* spike pairings. In the beginning, τ_w was short and w decayed quickly towards $w_\perp$. However, throughout the repeated experience of *pre-post* spike pairings, τ_w constantly grew so that w gradually decayed on slower time scales. In turn, this also

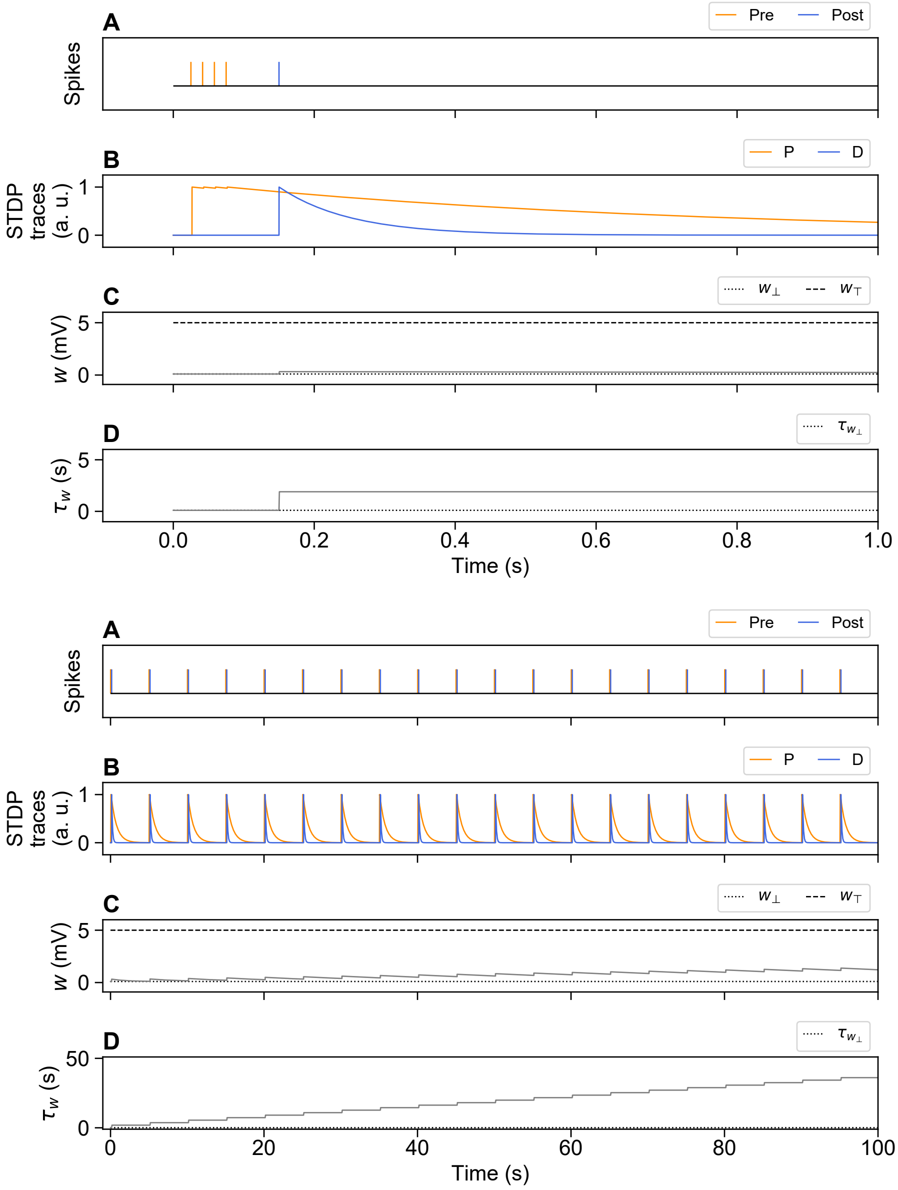


Figure 3.16: STDP synapse with SLMT experiencing a series of *pre-post* spike pairings. Zoom into the first second (**top**) and full simulation run (**bottom**). **A** Spikes at the synapse; Pre = presynaptic spikes; Post = postsynaptic spikes. **B** STDP traces; P = potentiation trace; D = depression trace. **C** Synaptic weight; $w_\perp$ = lower weight boundary; $w_\top$ = upper weight boundary. **D** Synaptic weight time constant; $\tau_{w_\perp}$ = lower weight time constant boundary. Synapse parameter space as in Lehfeldt et al. (n.d.), except for $D_{\perp\tau_w}$ = -1 s and $P_{\top\tau_w}$ = 2 s.

allowed w to grow as soon as the *pre-post* spike pairings, i.e. the potentiation events, occurred within temporal windows that were smaller than τ_w. As the growth of w was constantly hindered by the decay and depended on the growth of τ_w, learning at STDP synapses with SLMT took comparably longer as at STDP synapses. While w of a STDP synapse already approached $w_\top$ within the first 100 s of simulation (Fig. 3.13), w of a STDP synapse with SLMT still remained in a lower regime after the first

100 s of simulation (Fig. 3.16). Figure 3.17 further demonstrated that the growth of w in a STDP synapse with SLMT required substantially more time to approach $w_\top$, i.e. here approximately four times longer. Figure 3.18 demonstrated the dynamics of w during a Poisson pre- and postsynaptic input and showed that w in a STDP synapse with SLMT reached an elevated strength level but not the maximum, while w in a STDP synapse already saturated at $w_\top$ (Fig. 3.14). Finally, the influence of temporal gaps between *pre-post* spike pairings but also stimulus pauses between *post-pre* spike pairings was illustrated in Figure 3.19. With short temporal gaps, P was stronger at the onset of the postsynaptic spikes as compared to P with long temporal gaps. As a result, τ_w and w grew comparably stronger during the first potentiation event with a short gap. Further, with short stimulus pauses w had a shorter decay period until the occurrence of the next *pre-post* spike paring. Thus, w was at a comparably higher level when the second potentiation event occurred and consequently grew even stronger. Taken together, two consecutive *pre-post* input spike pairings with short gaps and pauses induced comparably stronger τ_w and w increases as compared to an input with long gaps and pauses. Even though with short pauses, also a notable decrease of τ_w and w occurred during the first *post-pre* spike pairings, this depression event did not outweigh the enhancing effect of short gaps and pauses.

3.2.5 Neuron and synapse variables at a glance

Next to the detailed demonstrations of individual model dynamics, all variables of excitatory LIF neurons with IP and plastic synapses were demonstrated at a glance in Figure 3.20 (STDP synapse) and Figure 3.21 (STDP synapse with SLMT). Here, again, the dynamics of variables were demonstrated in a small scale network where a pre- and postsynaptic excitatory LIF neuron both received individual Poisson spiking input. Further, pre- and postsynaptic LIF neurons were connected by a single plastic synapse.

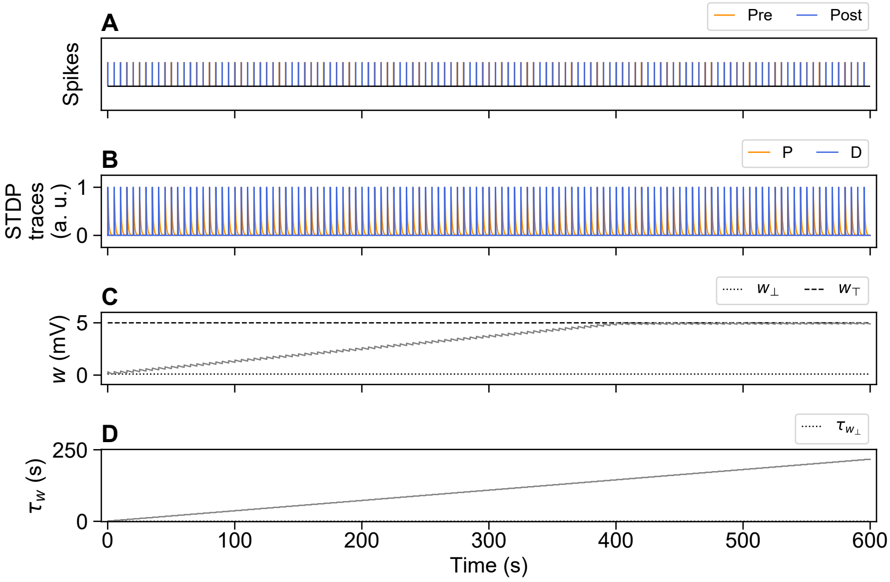


Figure 3.17: STDP synapse with SLMT experiencing a series of *pre-post* spike pairings. **A** Spikes at the synapse; Pre = presynaptic spikes; Post = postsynaptic spikes. **B** STDP traces; P = potentiation trace; D = depression trace. **C** Synaptic weight; $w_\perp$ = lower weight boundary; $w_\top$ = upper weight boundary. **D** Synaptic weight time constant; $\tau_{w_\perp}$ = lower weight time constant boundary. Synapse parameter space as in Lehfeldt et al. (n.d.), except for $D_{\perp\tau_w}$ = -1 s and $P_{\top\tau_w}$ = 2 s.

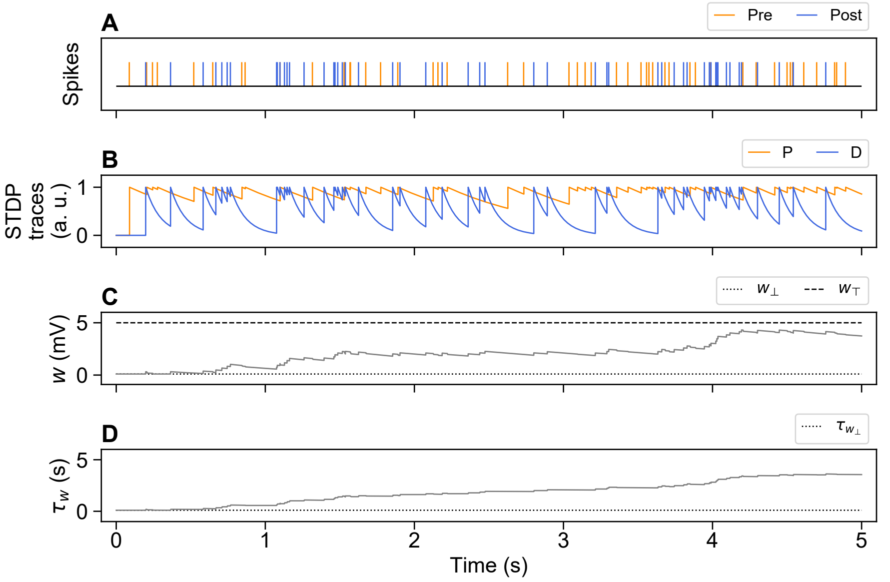


Figure 3.18: STDP synapse with SLMT experiencing a Poisson pre- and postsynaptic input. **A** Spikes at the synapse; Pre = presynaptic spikes; Post = postsynaptic spikes. **B** STDP traces; P = potentiation trace; D = depression trace. **C** Synaptic weight; $w_\perp$ = lower weight boundary; $w_\top$ = upper weight boundary. **D** Synaptic weight time constant; $\tau_{w_\perp}$ = lower weight time constant boundary. Synapse parameter space as in Lehfeldt et al. (n.d.), except for $D_{\perp\tau_w}$ = -0.05 s and $P_{\top\tau_w}$ = 0.1 s.

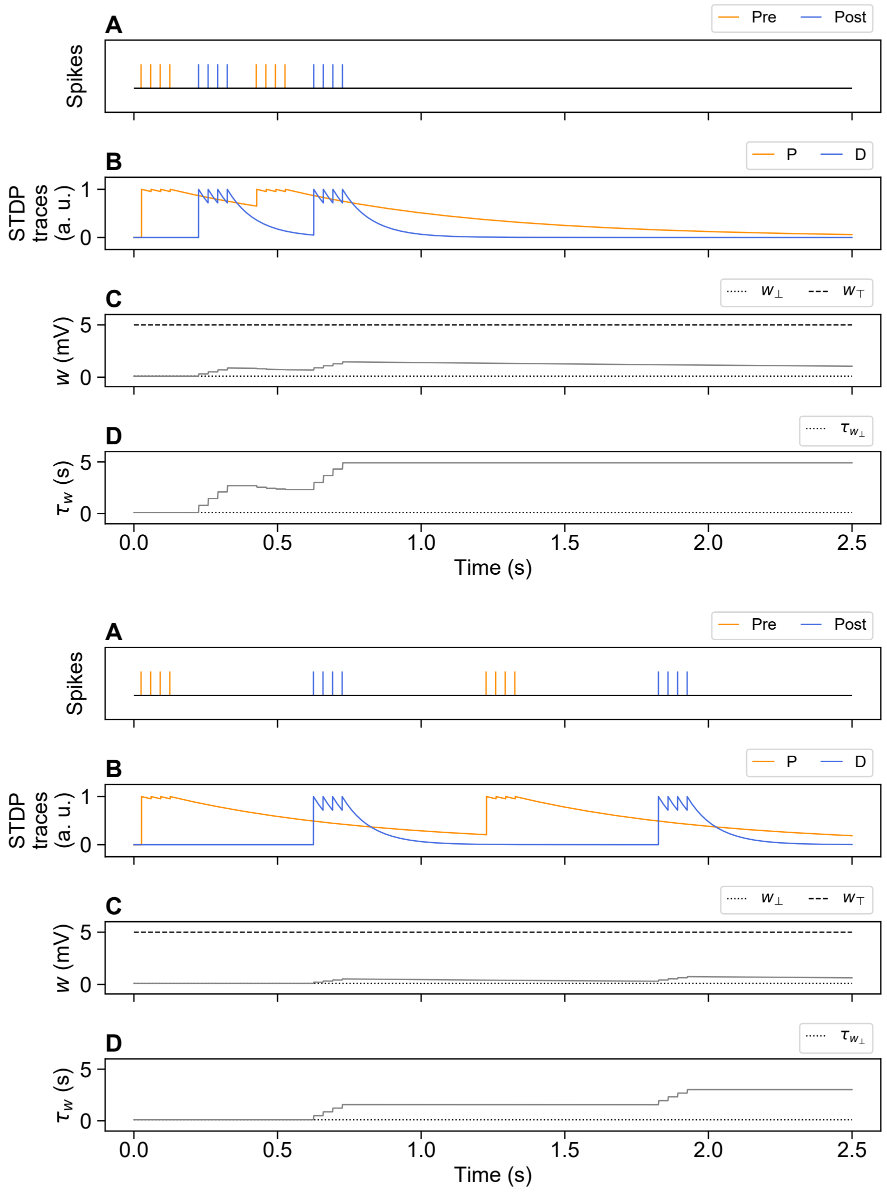


Figure 3.19: STDP synapse with SLMT experiencing *pre-post* and *post-pre* spike pairings with short and long temporal gaps/pauses. Comparably short (**top**) and long (**bottom**) temporal gaps/pauses. **A** Spikes at the synapse; Pre = presynaptic spikes; Post = postsynaptic spikes. **B** STDP traces; P = potentiation trace; D = depression trace. **C** Synaptic weight; $w_\perp$ = lower weight boundary; $w_\top$ = upper weight boundary. **D** Synaptic weight time constant; $\tau_{w_\perp}$ = lower weight time constant boundary. Synapse parameter space as in Lehfeldt et al. (n.d.), except for $D_{\perp\tau_w}$ = -0.4 s and $P_{\top\tau_w}$ = 0.8 s.

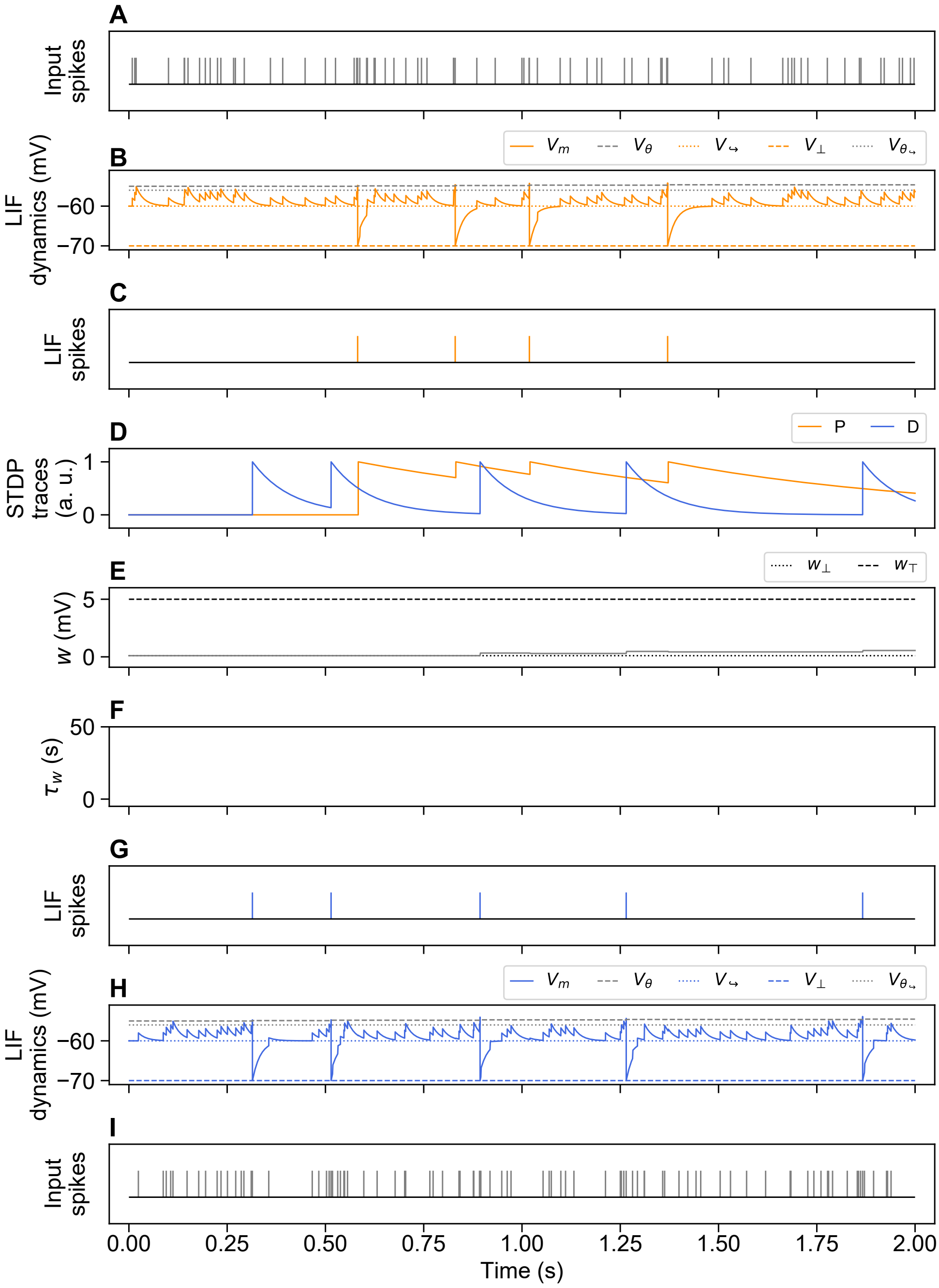


Figure 3.20: Variables of excitatory LIF neurons with IP and a STDP synapse. **A** Poisson input spikes to presynaptic LIF neuron. **B** Presynaptic LIF neuron variables. **C** Presynaptic LIF neuron output spikes. **D** Synaptic STDP traces. **E** Synaptic weight. **F** Synaptic weight time constant (empty here, as τ_w was not existent in a STDP synapse). **G** Postsynaptic LIF neuron output spikes. **H** Postsynaptic LIF neuron variables. **I** Poisson input spikes to postsynaptic LIF neuron. V_m = membrane voltage; V_θ = threshold voltage; $V_\hookrightarrow$ = resting voltage; $V_\perp$ = reset voltage; $V_{\theta_\hookrightarrow}$ = threshold resting voltage; P = potentiation trace; D = depression trace; $w_\perp$ = lower weight boundary; $w_\top$ = upper weight boundary. Neuron and synapse parameter spaces as in Lehfeldt et al. (n.d.).

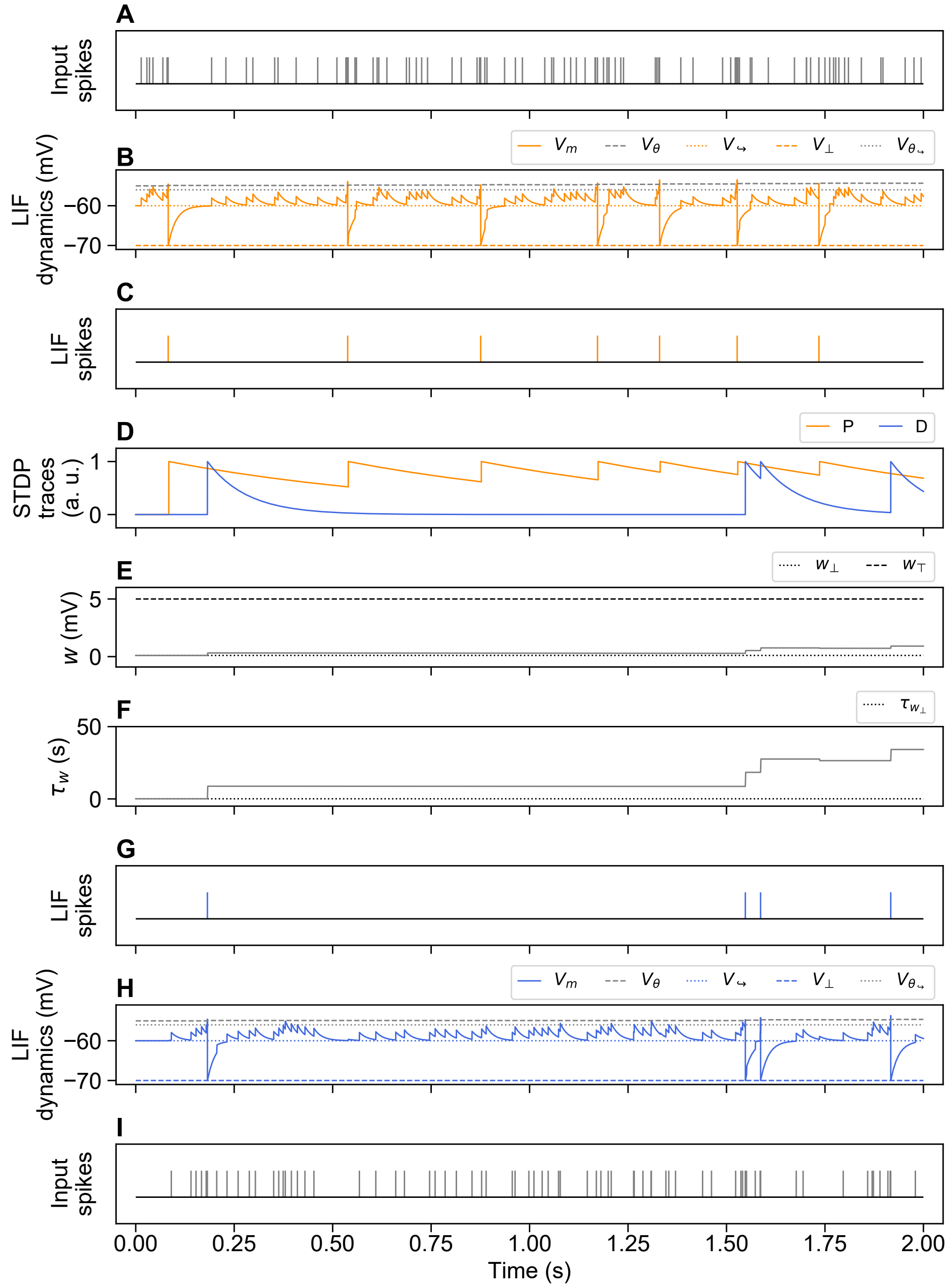


Figure 3.21: Variables of excitatory LIF neurons with IP and a STDP synapse with SLMT. **A** Poisson input spikes to presynaptic LIF neuron. **B** Presynaptic LIF neuron variables. **C** Presynaptic LIF neuron output spikes. **D** Synaptic STDP traces. **E** Synaptic weight. **F** Synaptic weight time constant. **G** Postsynaptic LIF neuron output spikes. **H** Postsynaptic LIF neuron variables. **I** Poisson input spikes to postsynaptic LIF neuron. V_m = membrane voltage; V_θ = threshold voltage; $V_{\hookrightarrow}$ = resting voltage; $V_\perp$ = reset voltage; $V_{\theta_{\hookrightarrow}}$ = threshold resting voltage; P = potentiation trace; D = depression trace; $w_\perp$ = lower weight boundary; $w_\top$ = upper weight boundary; $\tau_{w_\perp}$ = lower weight time constant boundary. Neuron and synapse parameter spaces as in Lehfeldt et al. (n.d.).

3.3 Grammar learning experiments: additional material

3.3.1 Spiking grammar sequences

In the grammar learning experiments (i.e. ‘X variability’, ‘X chunk size’, ‘Pause variability’ and ‘Emphasis’), isolated and nested NADs were presented as spiking sequences to the RNN. For details, see Sec. 3.1.2 ‘Spiking training sequences’ (Lehfeldt et al. n.d.). In the following, examples of spiking RNN activities during the grammar learning experiments were shown. Throughout, a zoom into the first 10 seconds of training was presented. Examples of experiment ‘X variability’ were shown for the conditions NL $=1$ and $N_X = 1$ (Fig. 3.22), NL $=2$ and $N_X = 5$ (Fig. 3.23) as well as NL $=3$ and $N_X = 15$ (Fig. 3.24). Examples of experiment ‘X chunk size’ were shown for the conditions NL $=1$ and $n_X = 0$ (Fig. 3.25), NL $=2$ and $n_X = 3$ (Fig. 3.26) as well as NL $=3$ and $n_X = 7$ (Fig. 3.27). Examples for experiment ‘Pause variability’ were shown for the conditions NL $=1$ and $\cup_\Delta = 0$ ms (Fig. 3.28), NL $=2$ and $\cup_\Delta = 300$ ms (Fig. 3.29) as well as NL $=3$ and $\cup_\Delta = 700$ ms (Fig. 3.30). An example for experiment ‘Emphasis’ was shown for the NL $=3$ condition (Fig. 3.31). For details on the set of grammatical stimuli, see Sec. 3.1.2 ‘Grammatical stimuli’ and for details on the grammar learning experiment conditions see Sec. 3.1.2 ‘Grammar learning experiments’ (Lehfeldt et al. n.d.). These figures illustrated how symbolic training sequences of AXB grammars were represented by the sequential and spike-based activation of stimulus element encoding input neurons. Further, they depicted the stimulus-driven spiking activity of the excitatory population which, in turn, triggered learning at the plastic EE synapses.

3.3.2 Synapse assembly types

For evaluation of the learning outcome, the strengths of stimulus element and transition encoding synapse assemblies in EE were analysed after training. An illustration of the different assembly types can be found in Fig. 3.1**E** (Lehfeldt et al. n.d.). Here, example snapshots of EE weight time constants and weights after training were shown, highlighting in colour the different assembly types. The stimulus element encoding synapse assemblies (i.e. A, X and B) were shown in Fig. 3.32. Grammatical A to B (i.e. $\lambda : A \rightarrow B$) and non-grammatical A to B (i.e. $\neg\lambda : A \rightarrow B$) and B to A (i.e. $B \rightarrow A$) transition assemblies were shown in Fig. 3.33. Non-grammatical A to A (i.e. $A \rightarrow A$), X to X (i.e. $X \rightarrow X$) and B to B (i.e. $B \rightarrow B$) transition assemblies were shown in Fig. 3.34. Finally, non-grammatical B to X (i.e. $B \rightarrow X$), X to A (i.e. $X \rightarrow A$) as well as non-assembly synapses (i.e. None) were shown in Fig. 3.35. The procedure to calculate the measure of successful learning from the assembly strength values was described in Sec. 3.1.2 ‘Separability measures’ (Lehfeldt et al. n.d.). The procedure for deriving separability measures of synaptic weights (w) applied equivalently to the synaptic weight time constants (τ_w).

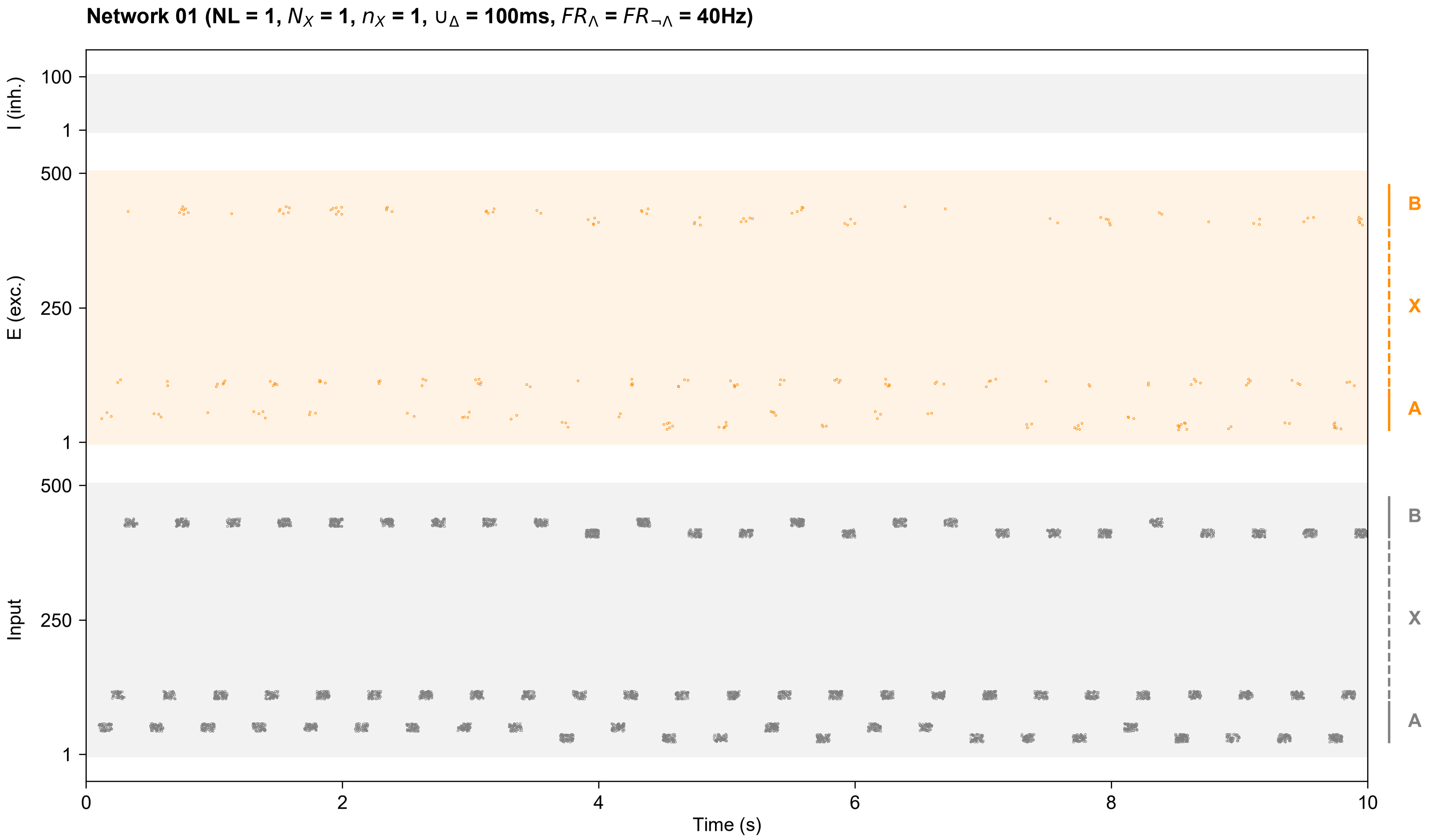


Figure 3.22: Example spiking network activity during training in experiment 'X variability' ($N_X = 1$). Zoom into the first 10 s of training; NL = nesting level; N_X = number of available X elements; n_X = number of X elements per grammar sample; $\cup_\Delta$ pause duration between grammar samples; FR = Poisson stimulus firing rate; Λ = grammatical neuron subgroups; $\neg\Lambda$ = non-grammatical neuron subgroups; Input = input population; E = excitatory population; I = inhibitory population; A = A element encoding subgroups; X = X element encoding subgroups; B = B element encoding subgroups.

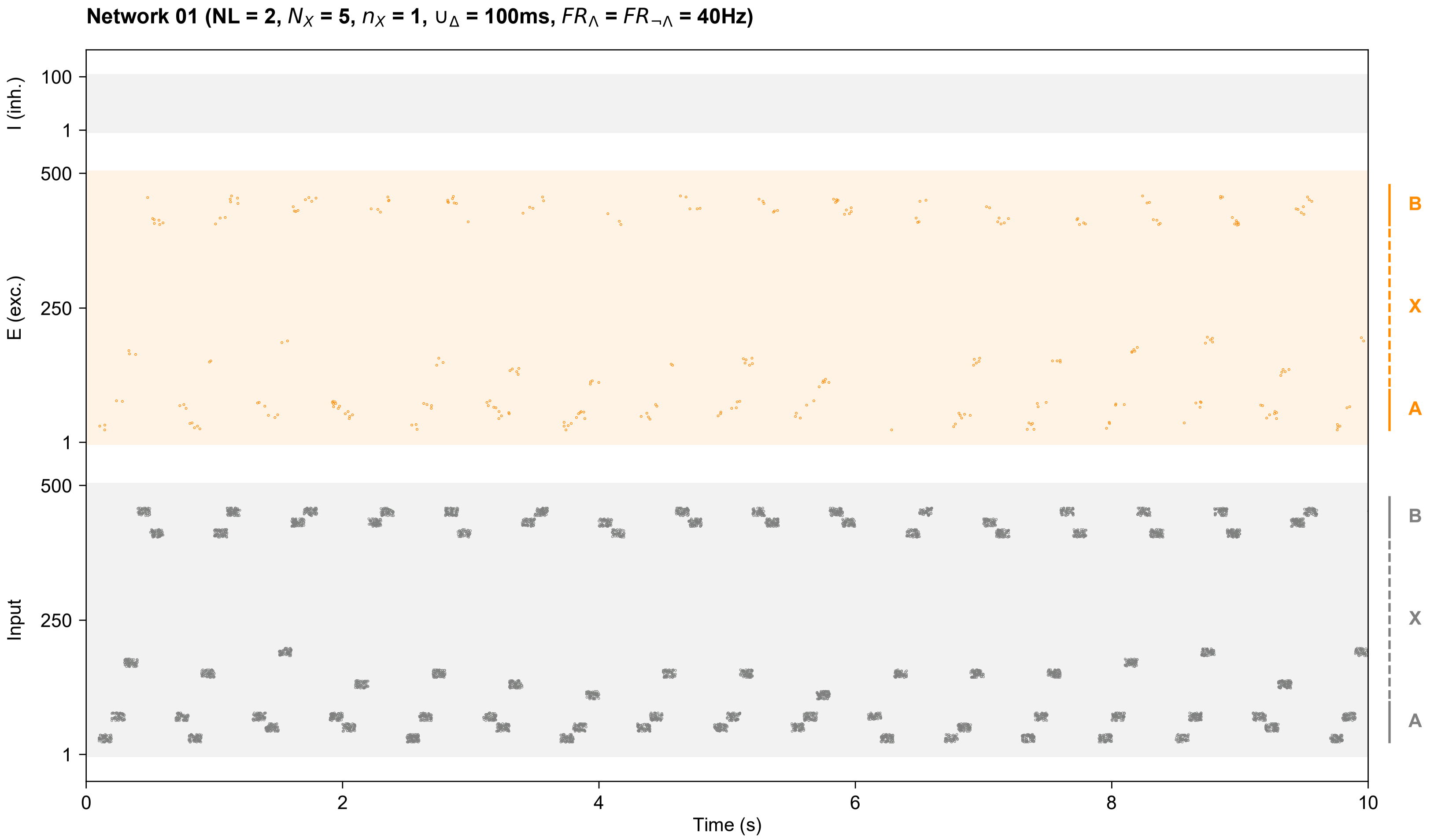


Figure 3.23: Example spiking network activity during training in experiment 'X variability' ($N_X = 5$). Zoom into the first 10 s of training; NL = nesting level; N_X = number of available X elements; n_X = number of X elements per grammar sample; $\cup_\Delta$ pause duration between grammar samples; FR = Poisson stimulus firing rate; Λ = grammatical neuron subgroups; $\neg\Lambda$ = non-grammatical neuron subgroups; Input = input population; E = excitatory population; I = inhibitory population; A = A element encoding subgroups; X = X element encoding subgroups; B = B element encoding subgroups.

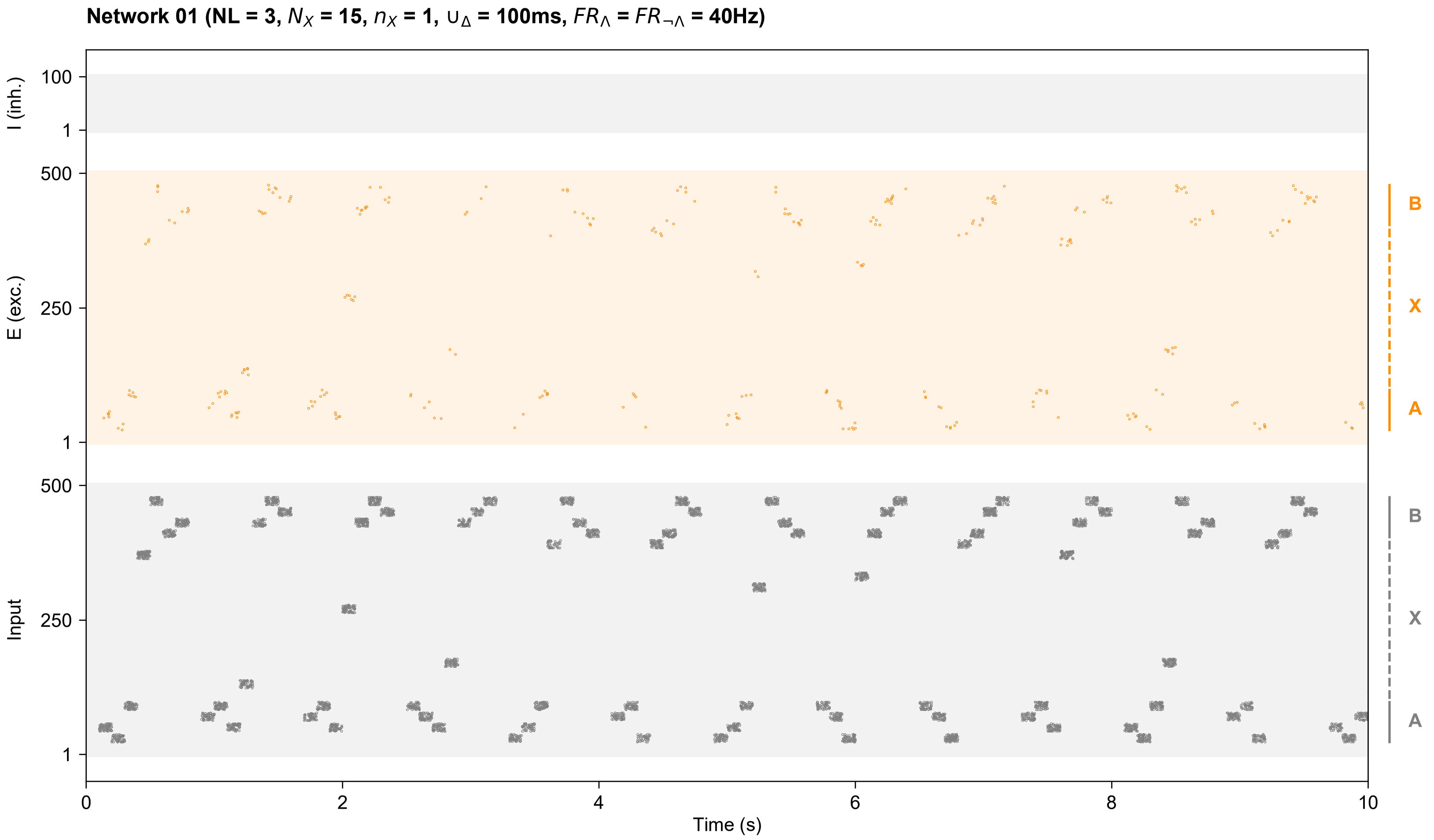


Figure 3.24: Example spiking network activity during training in experiment 'X variability' ($N_X = 15$). Zoom into the first 10 s of training; NL = nesting level; N_X = number of available X elements; n_X = number of X elements per grammar sample; $\cup_\Delta$ pause duration between grammar samples; FR = Poisson stimulus firing rate; Λ = grammatical neuron subgroups; $\neg\Lambda$ = non-grammatical neuron subgroups; Input = input population; E = excitatory population; I = inhibitory population; A = A element encoding subgroups; X = X element encoding subgroups; B = B element encoding subgroups.

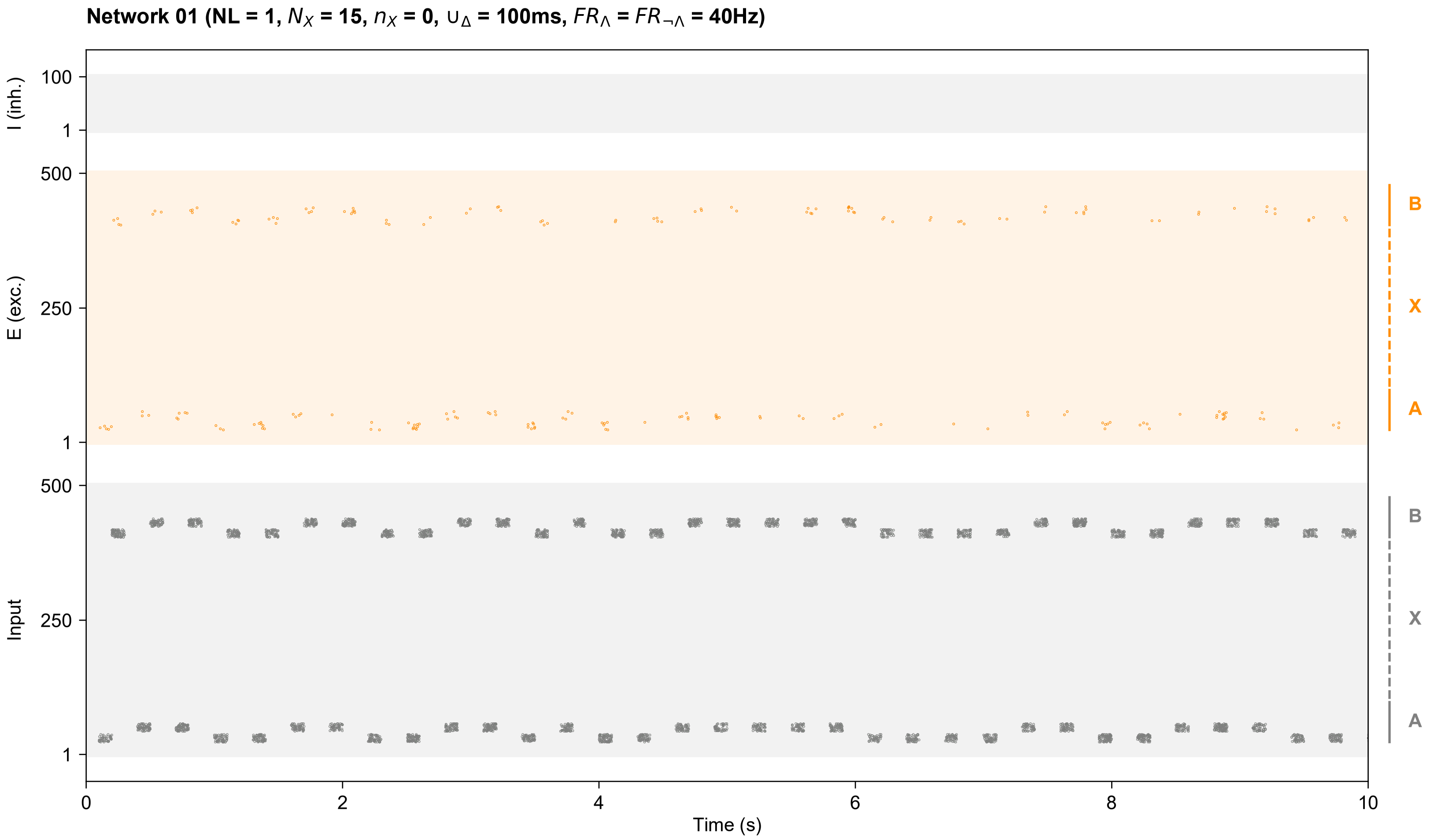


Figure 3.25: Example spiking network activity during training in experiment 'X chunk size' ($n_X = 0$). Zoom into the first 10 s of training; NL = nesting level; N_X = number of available X elements; n_X = number of X elements per grammar sample; $\cup_\Delta$ pause duration between grammar samples; FR = Poisson stimulus firing rate; Λ = grammatical neuron subgroups; $\neg\Lambda$ = non-grammatical neuron subgroups; Input = input population; E = excitatory population; I = inhibitory population; A = A element encoding subgroups; X = X element encoding subgroups; B = B element encoding subgroups.

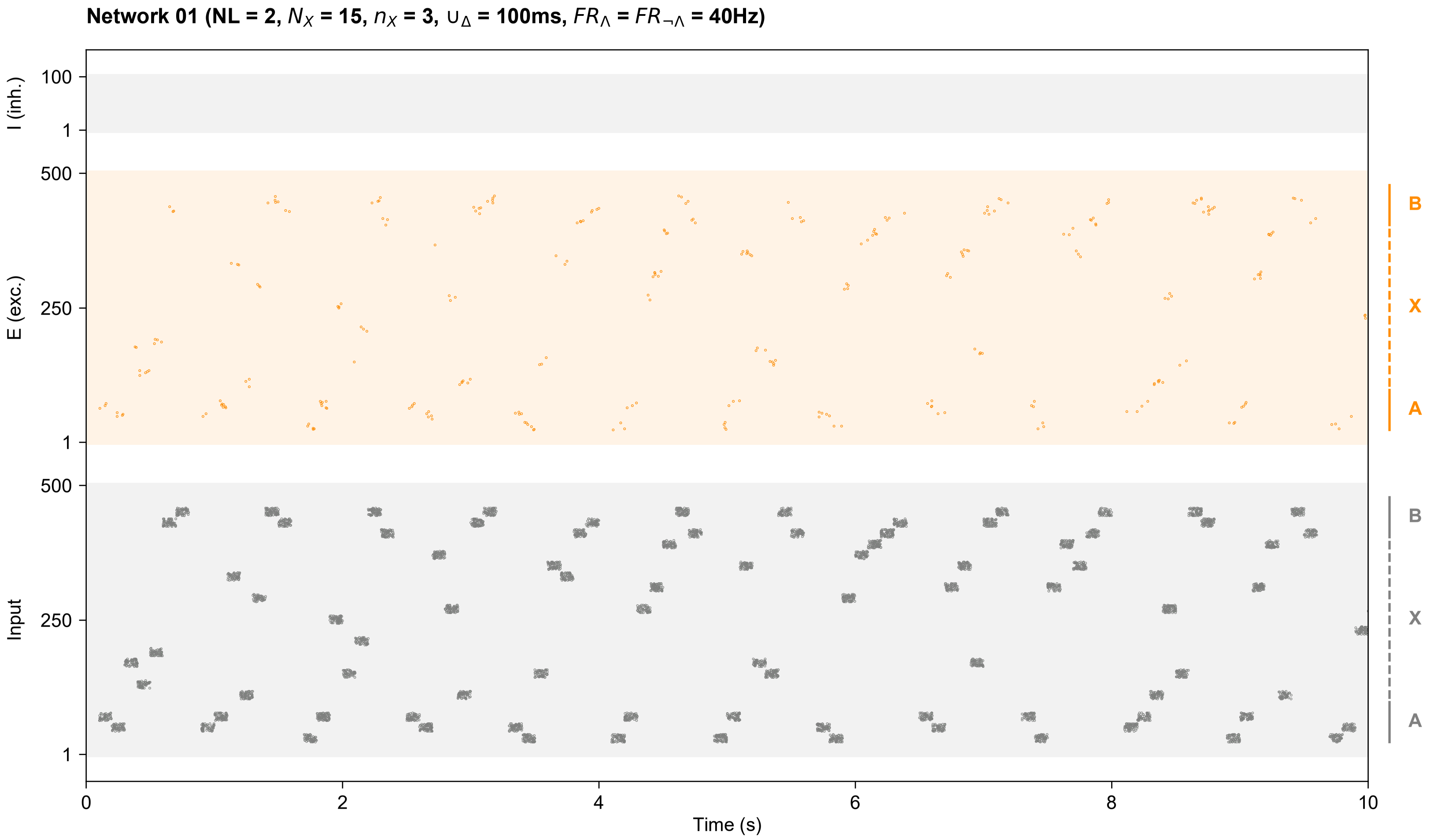


Figure 3.26: Example spiking network activity during training in experiment ‘X chunk size’ ($n_X = 3$). Zoom into the first 10 s of training; NL = nesting level; N_X = number of available X elements; n_X = number of X elements per grammar sample; $\cup_\Delta$ pause duration between grammar samples; FR = Poisson stimulus firing rate; Λ = grammatical neuron subgroups; $\neg\Lambda$ = non-grammatical neuron subgroups; Input = input population; E = excitatory population; I = inhibitory population; A = A element encoding subgroups; X = X element encoding subgroups; B = B element encoding subgroups.

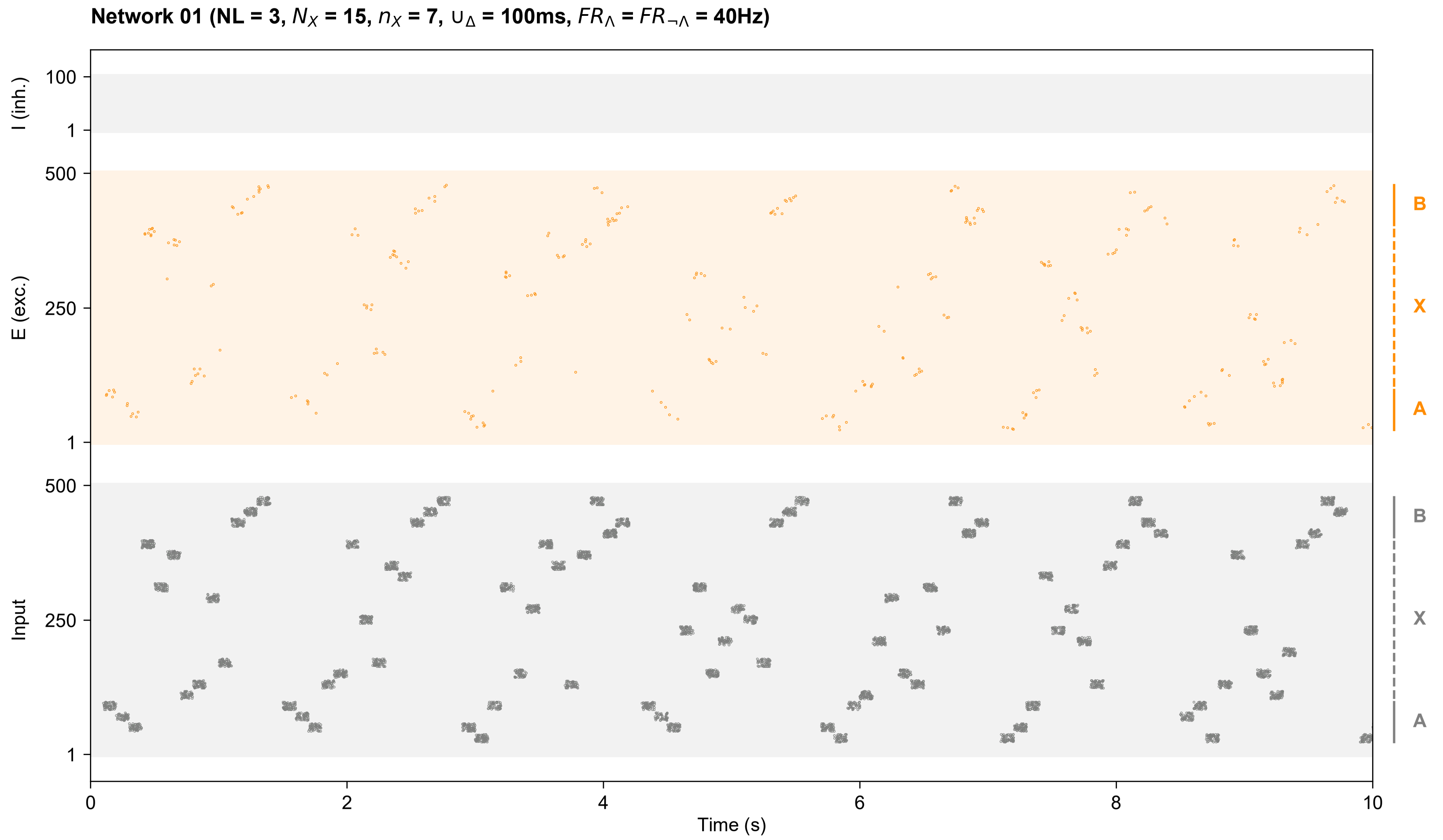


Figure 3.27: Example spiking network activity during training in experiment 'X chunk size' (n_X = 7). Zoom into the first 10 s of training; NL = nesting level; N_X = number of available X elements; n_X = number of X elements per grammar sample; $\cup_\Delta$ pause duration between grammar samples; FR = Poisson stimulus firing rate; Λ = grammatical neuron subgroups; $\neg\Lambda$ = non-grammatical neuron subgroups; Input = input population; E = excitatory population; I = inhibitory population; A = A element encoding subgroups; X = X element encoding subgroups; B = B element encoding subgroups.

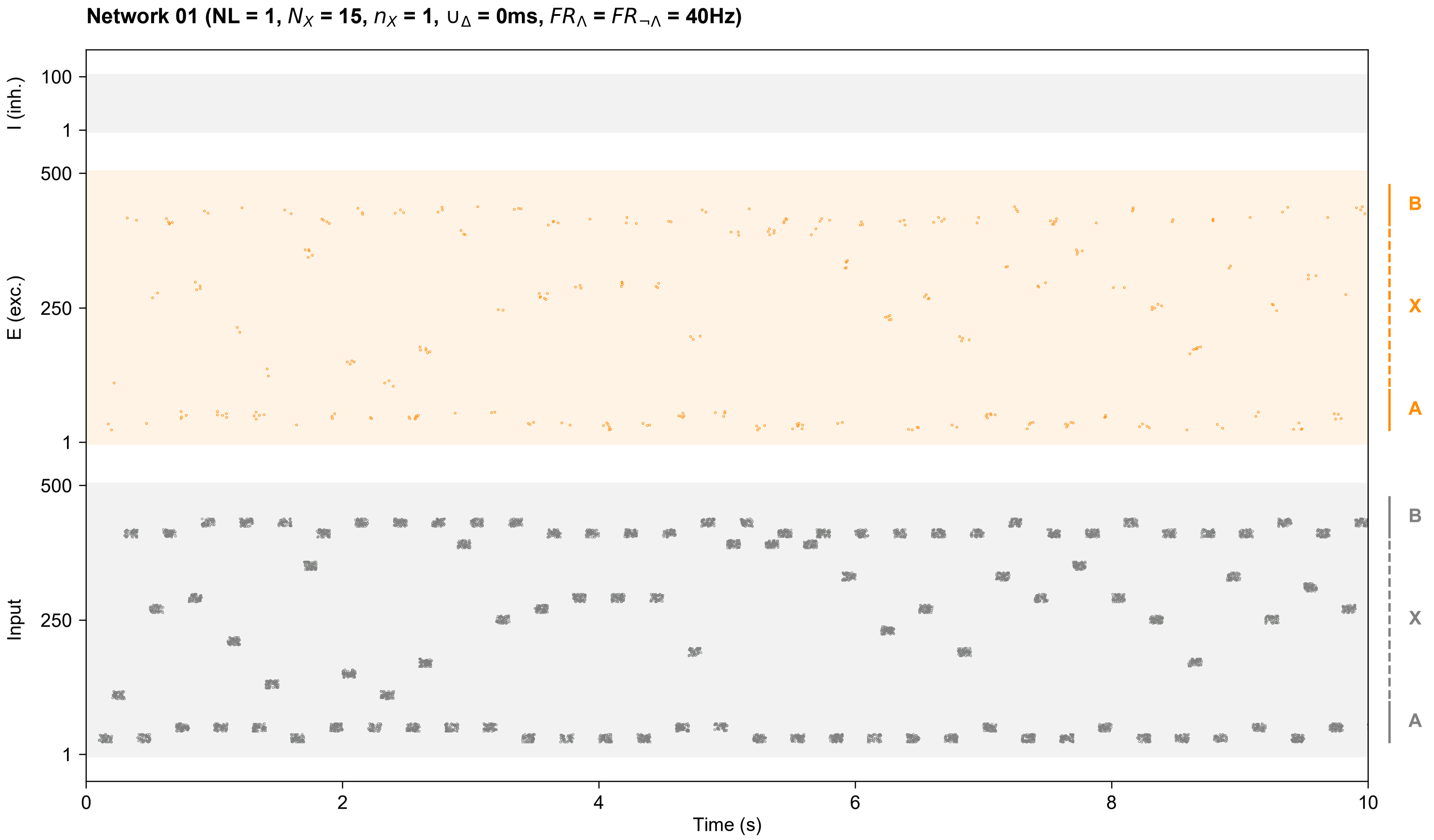


Figure 3.28: Example spiking network activity during training in experiment 'Pause variability' ($\cup_\Delta = 0$ ms). Zoom into the first 10 s of training; NL = nesting level; N_X = number of available X elements; n_X = number of X elements per grammar sample; $\cup_\Delta$ pause duration between grammar samples; FR = Poisson stimulus firing rate; Λ = grammatical neuron subgroups; $\neg\Lambda$ = non-grammatical neuron subgroups; Input = input population; E = excitatory population; I = inhibitory population; A = A element encoding subgroups; X = X element encoding subgroups; B = B element encoding subgroups.

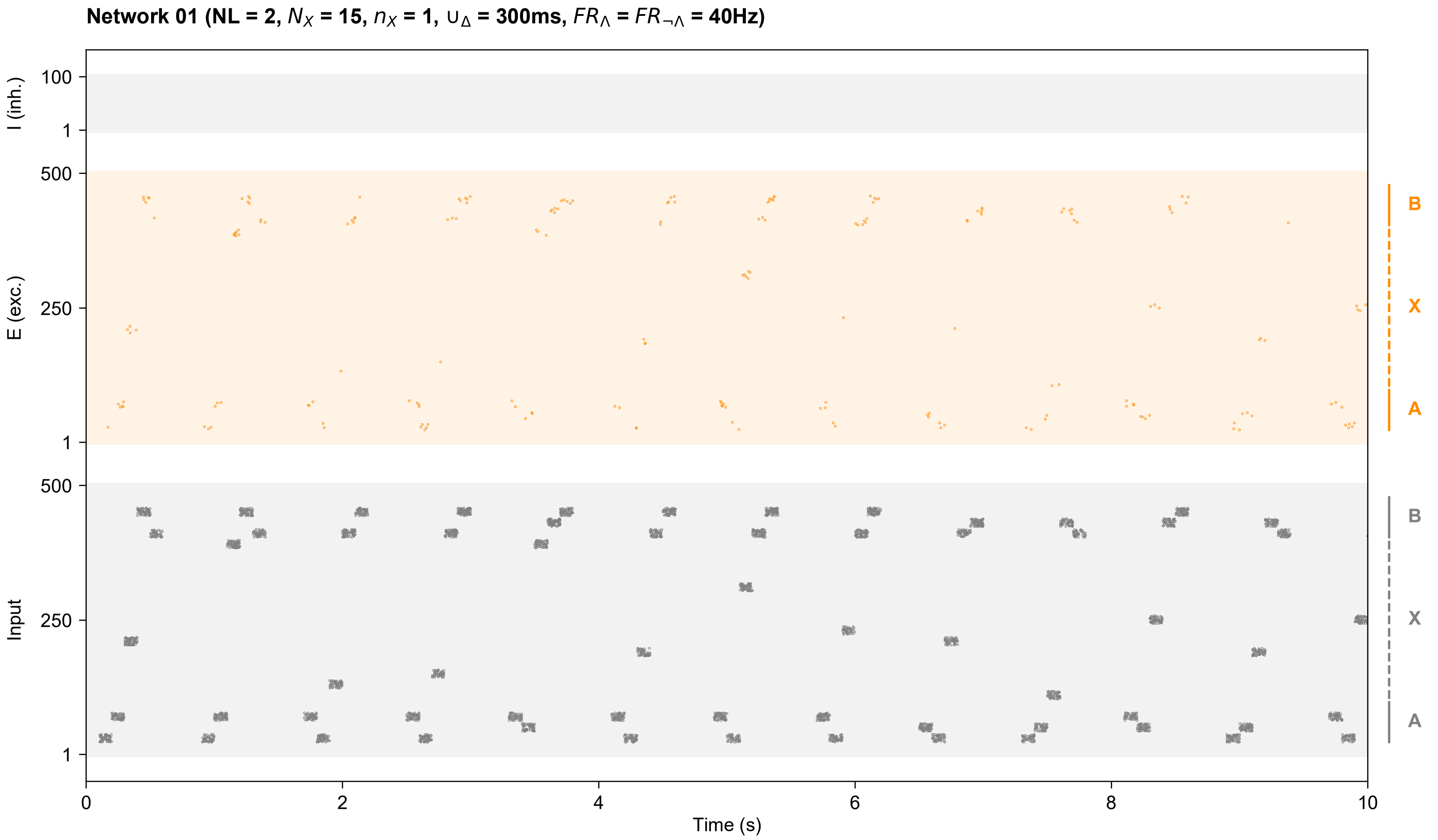


Figure 3.29: Example spiking network activity during training in experiment 'Pause variability' ($\cup_\Delta = 300$ ms). Zoom into the first 10 s of training; NL = nesting level; N_X = number of available X elements; n_X = number of X elements per grammar sample; $\cup_\Delta$ pause duration between grammar samples; FR = Poisson stimulus firing rate; Λ = grammatical neuron subgroups; $\neg\Lambda$ = non-grammatical neuron subgroups; Input = input population; E = excitatory population; I = inhibitory population; A = A element encoding subgroups; X = X element encoding subgroups; B = B element encoding subgroups.

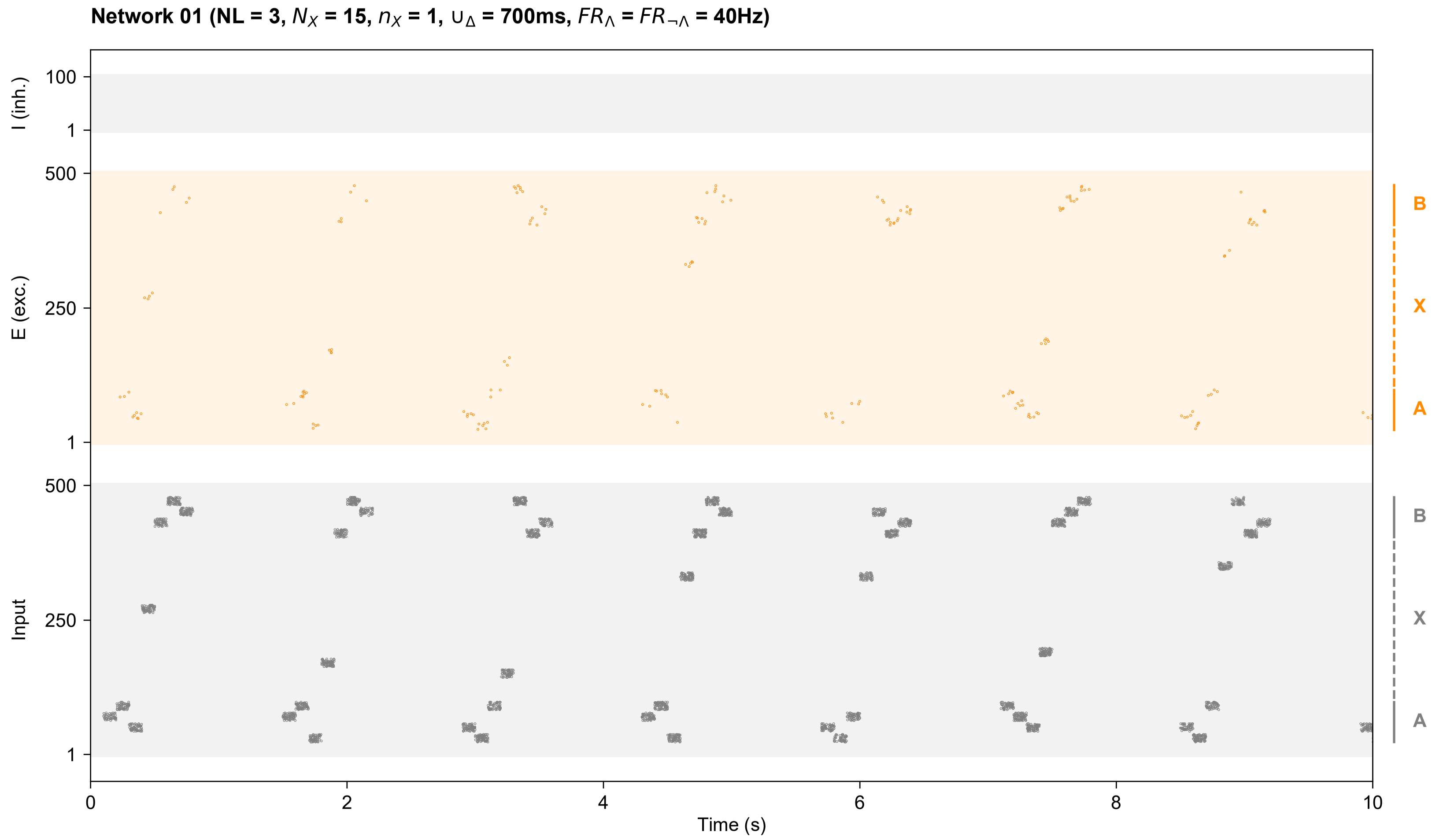


Figure 3.30: Example spiking network activity during training in experiment 'Pause variability' ($\cup_\Delta = 700$ ms). Zoom into the first 10 s of training; NL = nesting level; N_X = number of available X elements; n_X = number of X elements per grammar sample; $\cup_\Delta$ pause duration between grammar samples; FR = Poisson stimulus firing rate; Λ = grammatical neuron subgroups; $\neg\Lambda$ = non-grammatical neuron subgroups; Input = input population; E = excitatory population; I = inhibitory population; A = A element encoding subgroups; X = X element encoding subgroups; B = B element encoding subgroups.

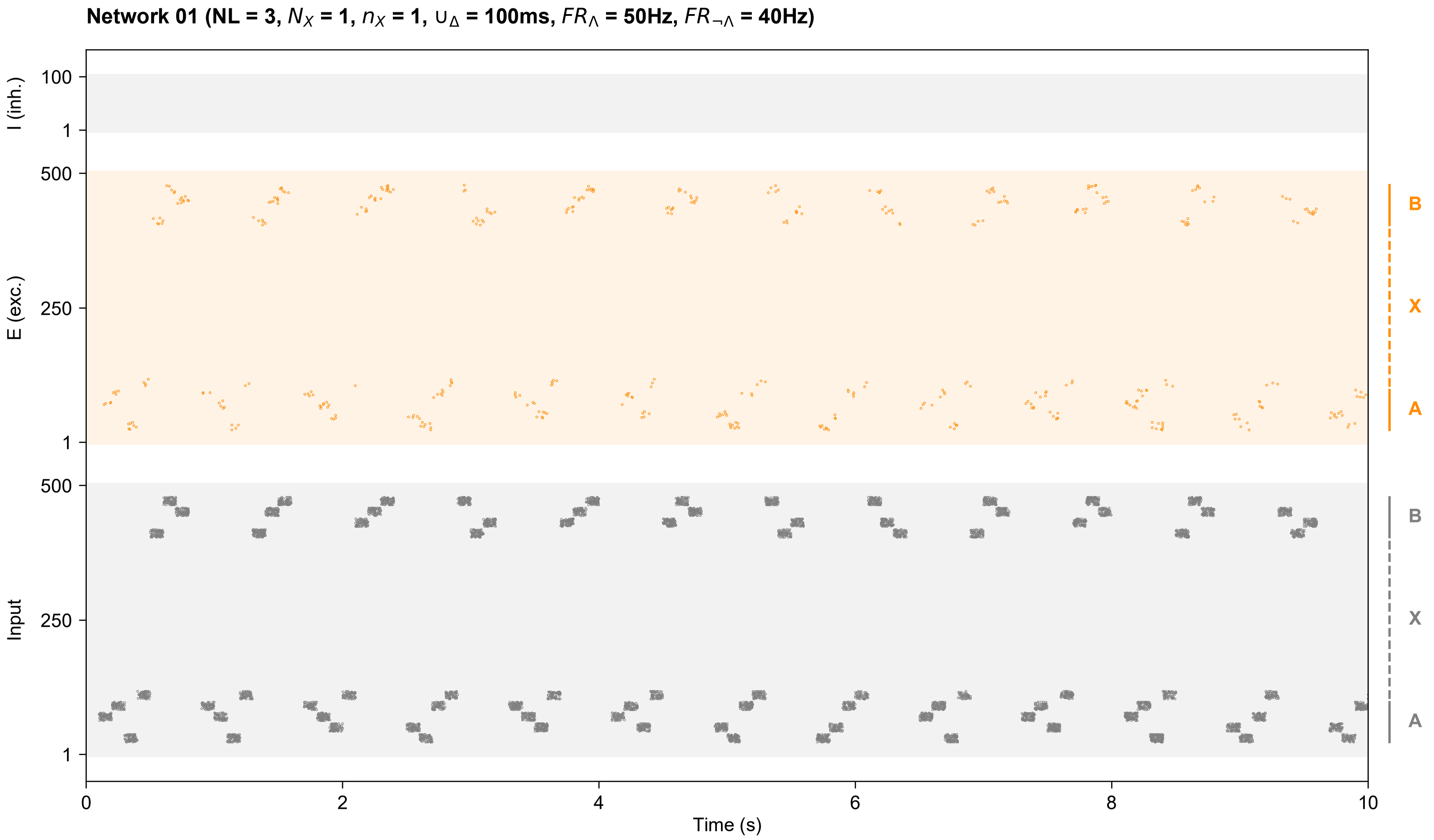


Figure 3.31: Example spiking network activity during training in experiment ‘Emphasis’. Zoom into the first 10 s of training; NL = nesting level; N_X = number of available X elements; n_X = number of X elements per grammar sample; $\cup_\Delta$ pause duration between grammar samples; FR = Poisson stimulus firing rate; Λ = grammatical neuron subgroups; $\neg\Lambda$ = non-grammatical neuron subgroups; Input = input population; E = excitatory population; I = inhibitory population; A = A element encoding subgroups; X = X element encoding subgroups; B = B element encoding subgroups.

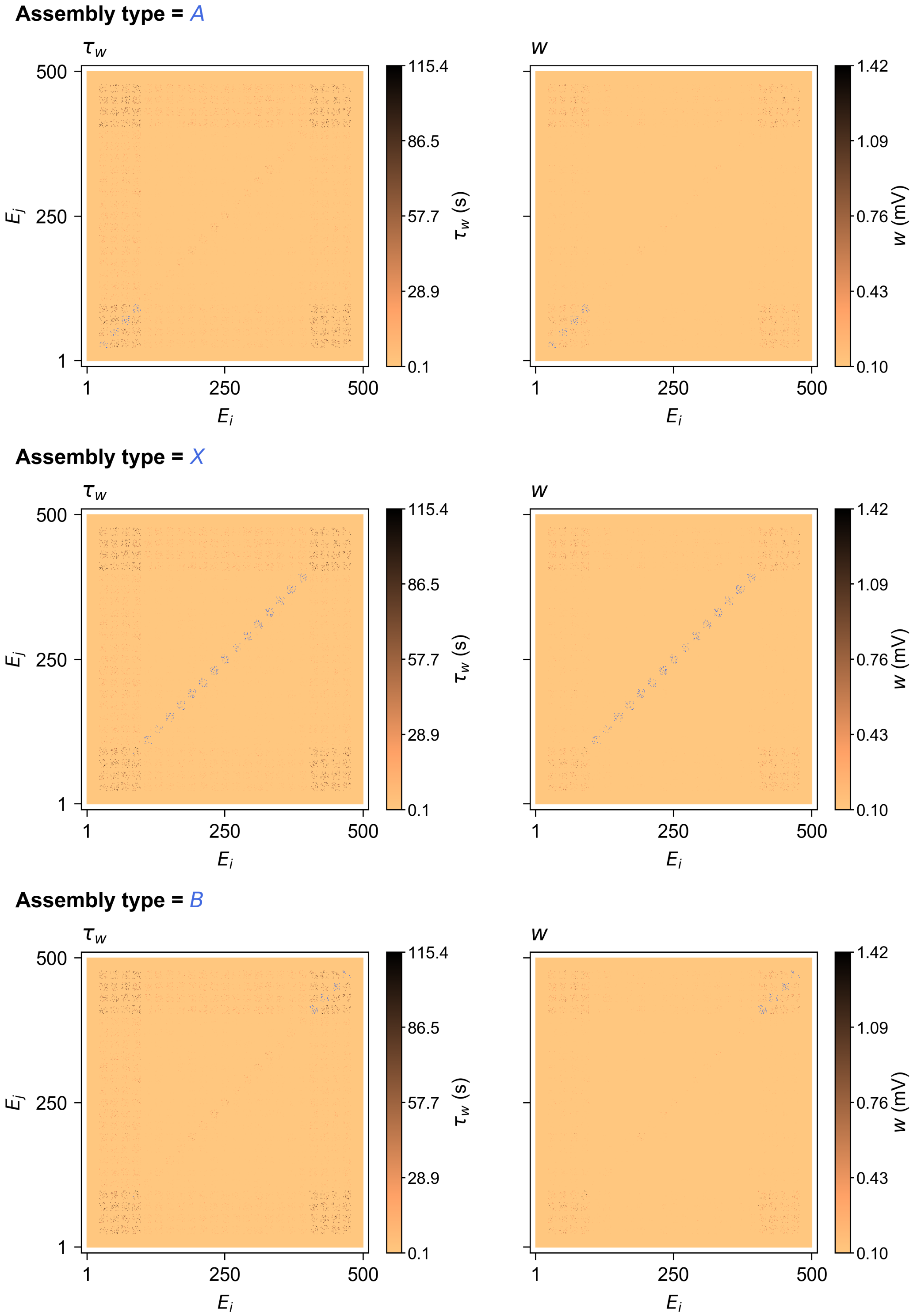


Figure 3.32: Element encoding synapse assemblies A, X and B. Example synaptic EE snapshot (E_i = source/pre, E_j = target/post) after training (NL = 3, experiment 'X variability', $N_X = 15$) with highlighted assembly types by colour (blue); assembly type indicated above each row; left column: weight time constant (τ_w); right column: weight (w).

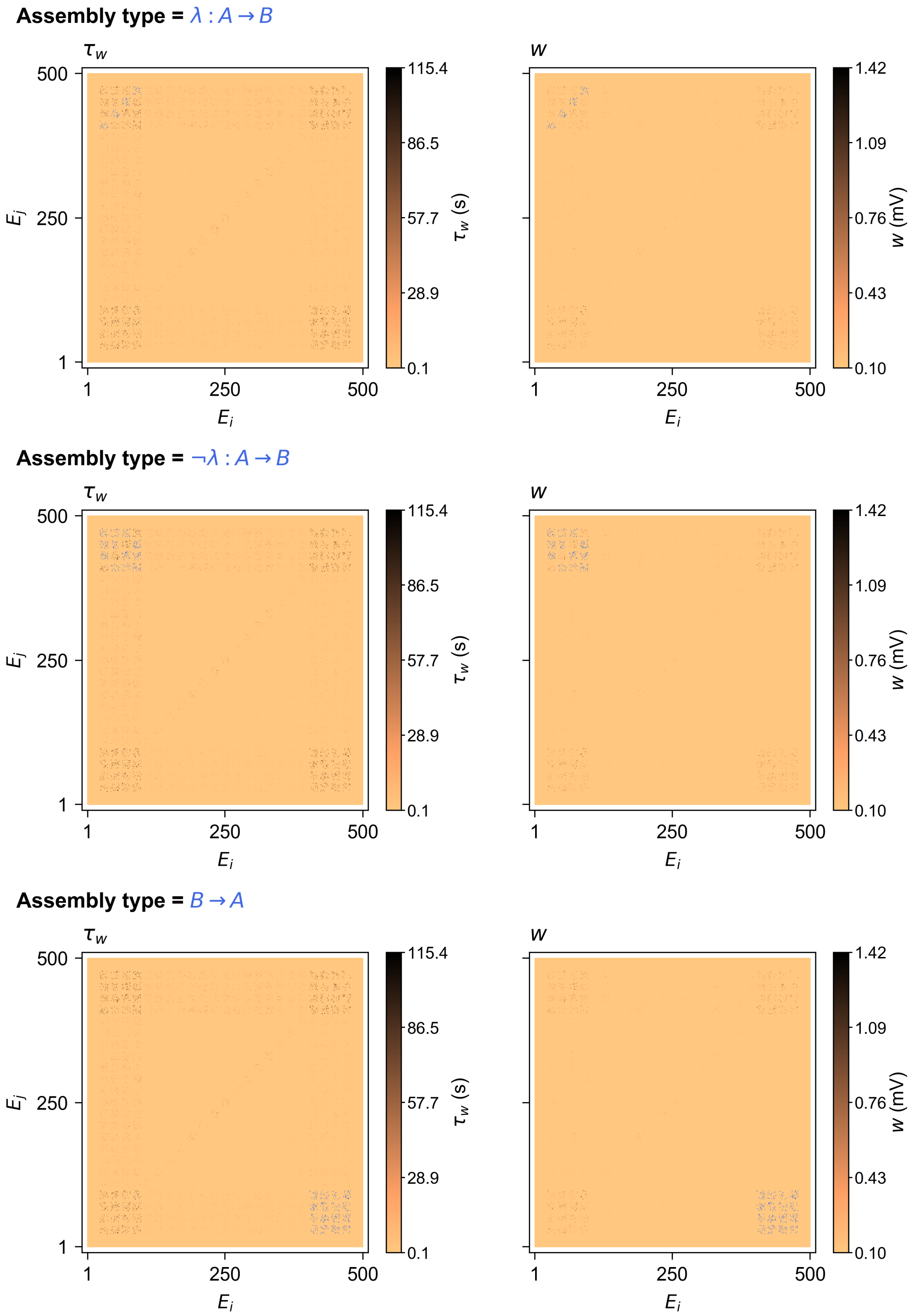


Figure 3.33: Transition encoding synapse assemblies $\lambda : A \rightarrow B$, $\neg\lambda : A \rightarrow B$ and $B \rightarrow A$. Example synaptic EE snapshot (E_i = source/pre, E_j = target/post) after training (NL = 3, experiment 'X variability', $N_X = 15$) with highlighted assembly types by colour (blue); assembly type indicated above each row; left column: weight time constant (τ_w); right column: weight (w).

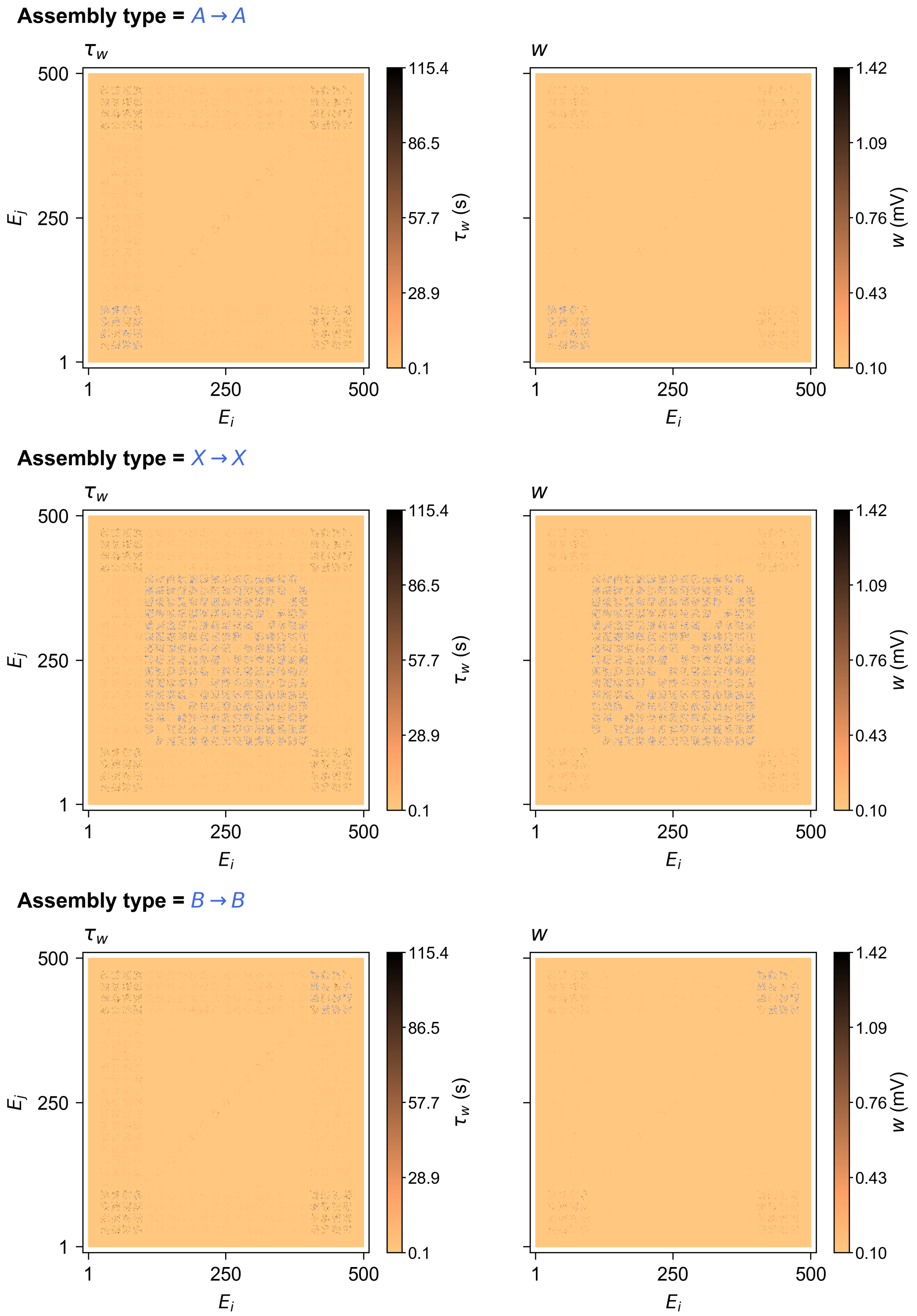


Figure 3.34: Transition encoding synapse assemblies $A \rightarrow A$, $X \rightarrow X$ and $B \rightarrow B$. Example synaptic EE snapshot (E_i = source/pre, E_j = target/post) after training (NL = 3, experiment 'X variability', $N_X = 15$) with highlighted assembly types by colour (blue); assembly type indicated above each row; left column: weight time constant (τ_w); right column: weight (w).

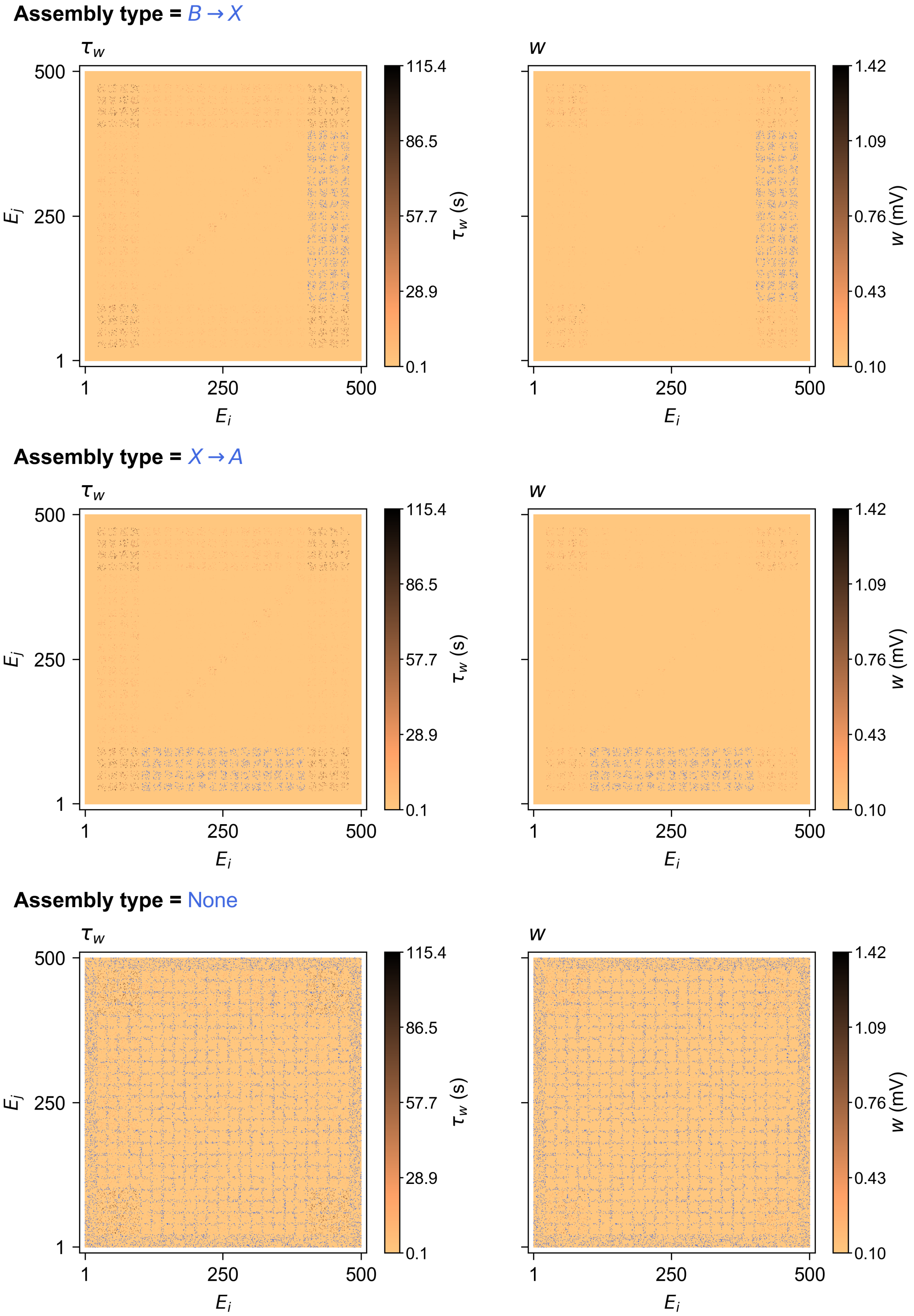


Figure 3.35: Transition encoding synapse assemblies $B \to X$, $X \to A$ and *None*. Example synaptic EE snapshot (E_i = source/pre, E_j = target/post) after training (NL = 3, experiment 'X variability', $N_X = 15$) with highlighted assembly types by colour (blue); assembly type indicated above each row; left column: weight time constant (τ_w); right column: weight (w).

3.3.3 Assembly dynamics

3.3.3.1 Complete collection of assembly dynamics

The full collection of synaptic weight (w) dynamics across experiments and RNNs was shown in Fig. 3.5 to Fig. 3.8 (Lehfeldt et al. n.d.). Here, additionally the corresponding and complete collection of assembly weight time constant (τ_w) dynamics were presented (Fig. 3.36, Fig. 3.37, Fig. 3.38 and Fig. 3.39). The synaptic state variable τ_w followed the same spike-triggered update routines as w, though with a different parameter space. For details, see Sec. 3.1.2 'Spike-timing dependent plasticity (STDP) with short- to long-term memory transition (SLMT)' (Lehfeldt et al. n.d.). Thus, qualitatively similar τ_w dynamics across the experiment conditions occurred when compared to w. However, as τ_w was temporally infinite, i.e. had no decay itself, it occasionally showed different dynamics for stimulus conditions that modified temporal gaps between stimulus element occurrences and transitions. In the following, τ_w dynamics were thus shortly described and explained in comparison to w, highlighting shared and different dynamics between them. Again, assembly dynamics across grammars and experimental conditions were fully explained by the sensitivity of STDP and SLMT to stimulus element order, temporal proximity, occurrence frequency and strength (Lehfeldt et al. n.d.). For a detailed description and explanation of w dynamics, see Sec. 3.1.2 'Results' and Sec. 3.1.2 'Discussion' (Lehfeldt et al. n.d.). Taken together, the full collection of w and τ_w dynamics provided a complete view onto the modelled learning dynamics. This further highlighted the benefit of the model, namely the possibility to study the full bandwidth of stimulus element and transition dynamics.

3.3.3.2 Experiment 'X variability': assembly dynamics

In experiment 'X variability', both τ_w and w showed qualitatively equal dynamics across the N_X conditions (τ_w: Fig. 3.36 and w: Fig. 3.5). While those assemblies that were independent from the X variability remained constant, dependent assemblies (i.e. the sets $\chi : \{A \rightarrow X,\, X,\, X \rightarrow B\}$ and $\chi' : \{X \rightarrow X,\, B \rightarrow X,\, X \rightarrow A\}$) decreased over increasing X variabilities. The decrease of χ and χ' assembly weights was explained by decreased occurrence frequencies of individual X elements under high X variabilities (Lehfeldt et al. n.d.). This effect equally applied to τ_w (τ_w: Fig. 3.36**E**,**F** and w: Fig. 3.5**E**,**F**). However, different dynamics in w and τ_w occurred for the remaining assembly types and across grammar complexities, i.e. nesting levels (NLs). Across NLs, w of $\lambda : A \rightarrow B$, A, B and $B \rightarrow A$ assemblies remained largely at the same strength levels (Fig. 3.5**A**,**B**,**G**). In $\neg\lambda : A \rightarrow B$ and the set $\widehat{AA}\widehat{BB} : \{A \rightarrow A,\, B \rightarrow B\}$, w showed an increase between isolated and nested NADs (Fig. 3.5**C**,**D**). However, τ_w had consistently increasing strength levels across NLs and in all theses assembly types (Fig. 3.36**A**-**D**, **G**). These increases were explained by consistently increasing A and B element occurrence frequencies across NLs (Fig. 3.4**A**). While the temporally infinite τ_w represented different occurrence frequencies in the training sequences accordingly, the decay of w compensated this frequency effect. As a result, w assembly strengths remained largely constant across NLs or only increased between isolated and nested NADs.

3.3.3.3 Experiment 'X chunk size': assembly dynamics

In experiment 'X chunk size', τ_w and w showed qualitatively equal dynamics for $\lambda : A \rightarrow B$, $\neg\lambda : A \rightarrow B$, χ and χ' (τ_w: Fig. 3.37 and w: Fig. 3.6). In both, $\lambda : A \rightarrow B$ and $\neg\lambda : A \rightarrow B$ decreased over the n_X conditions, while χ and χ' increased (τ_w: Fig. 3.37**A**,**C**,**E**,**F** and w: Fig. 3.6**A**,**C**,**E**,**F**). These effects in w were explained by increased within-sample temporal gaps of A to B element transitions and increased occurrence frequencies of X elements (Lehfeldt et al. n.d.). These effects equally applied to τ_w. However, different dynamics in w and τ_w occurred for the remaining assemblies. While A and B in w decreased over the n_X conditions, they remained constant or slightly increased in τ_w (τ_w: Fig. 3.37**B** and w: Fig. 3.6**B**). Here, increased temporal gaps between A and B element occurrences resulted in prolonged decay periods of w, while the temporally infinite τ_w was not affected. The $\widehat{AABB}$ assemblies decreased consistently in w while in τ_w, they decreased the strongest for NL = 1 grammars, decreased comparably weaker for NL = 2 grammars and remained constant for NL = 3 grammars (τ_w: Fig. 3.37**D** and w: Fig. 3.6**D**). The consistent decrease of w was explained by prolonged decay periods across n_X conditions. However, the dynamics of temporally infinite τ_w were explained by the structural composition of grammars. In isolated NADs, $A \rightarrow A$ and $B \rightarrow B$ transitions could only grow due to cross-sample interference (Lehfeldt et al. n.d.). Thus, their growth was negatively affected by increased temporal gaps induced by large n_X. This effect, however, decreased with increasing grammar complexities given that in nested NADs, $A \rightarrow A$ and $B \rightarrow B$ transitions already existed within individual grammar samples. Finally, $B \rightarrow A$ assemblies in w decreased for isolated NADs but remained largely constant for nested NADs while in τ_w, they consistently increased across n_X conditions (τ_w: Fig. 3.37**G** and w: Fig. 3.6**G**). These dynamics in τ_w were explained by a decreased amount of cross-sample depression in $B \rightarrow A$. In general, during the experience of an A to B transition, potentiation occurred in $\lambda : A \rightarrow B$ while depression occurred in $B \rightarrow A$ (Lehfeldt et al. n.d.). Thus, for large n_X, the amount of depression was reduced by longer decay periods of A element depression traces in $B \rightarrow A$, resulting in a stronger $B \rightarrow A$ growth. In w, however, the weight decay again compensated for this effect in nested NADs. Further, the decrease of $B \rightarrow A$ in isolated NADs was explained by prolonged decay periods of w between potentiation events (i.e. cross-sample B to A transitions), that were induced by longer grammar samples. As isolated NADs consisted of only one grammatical A and B pair, this effect was the strongest here.

3.3.3.4 Experiment 'Pause variability': assembly dynamics

In experiment 'Pause variability', τ_w and w showed qualitatively equal dynamics for $\lambda : A \rightarrow B$, χ and $B \rightarrow A$ (τ_w: Fig. 3.38 and w: Fig. 3.7). In both, $\lambda : A \rightarrow B$ increased over increasing pause durations while this effect was stronger in τ_w (τ_w: Fig. 3.38**A** and w: Fig. 3.7**A**). The consistent increase was explained by decreased amounts of cross-sample depression (Lehfeldt et al. n.d.). As τ_w had no decay, this effect was more pronounced here. In χ, τ_w and w were constant across pause durations, whereby assemblies in w remained at the baseline level (τ_w: Fig. 3.38**E** and w: Fig. 3.7**E**). In τ_w, the consistency of within-sample χ was explained by the temporal infinity of τ_w and hence, by its independence from between-sample pause durations. In w, χ assemblies remained at the baseline level as the 'Pause variability' experiment was conducted in the $N_X = 15$ variability condition. Cross-sample $B \rightarrow A$ in w and τ_w decreased consistently across pause durations (τ_w: Fig. 3.38**G** and w: Fig. 3.7**G**). This effect was explained by prolonged decay periods of potentiation traces induced by long pauses and hence, reduced amounts of cross-sample potentiation. However, different dynamics in w and τ_w occurred for the remaining assembly types. In A and B, strengths remained largely constant across pause durations in τ_w while in w, they consistently decreased (τ_w: Fig. 3.38**B** and w: Fig. 3.7**B**). Further, A and B reached higher strength levels across grammar complexities in τ_w, which was explained by increased occurrence frequencies of A and B elements in nested NADs (Fig. 3.4**C**). The consistency of A and B in τ_w was again explained by its temporal infinity while in w, the decrease was explained by prolonged decay periods. In $\neg\lambda : A \rightarrow B$, both w and τ_w decreased in isolated NADs while in nested NADs, w remained largely constant and τ_w increased (τ_w: Fig. 3.38**C** and w: Fig. 3.7**C**). The decrease of $\neg\lambda : A \rightarrow B$ in isolated NADs was explained by decreased amounts of cross-sample potentiation due to long stimulus pauses and hence, long decay periods of potentiation traces. In τ_w, the consistent increase across pause durations was explained by decreased amounts of cross-sample depression whereby in w, this effect was counteracted by the weight decay. In $\widehat{AA}\widehat{BB}$, w consistently decreased over pause durations while τ_w decreased the most for isolated NADs and subsequently less for nested NADs (τ_w: Fig. 3.38**D** and w: Fig. 3.7**D**). The decrease in w was again explained by prolonged decay periods due to long pauses. In τ_w, dynamics were explained by the structural composition of grammars, whereby in isolated NADs the effect of reduced amounts of cross-sample potentiation was the strongest. In χ', assembly strengths slightly decreased or remained at baseline level in τ_w, while they fully remained at baseline level in w (τ_w: Fig. 3.38**F** and w: Fig. 3.7**F**). χ' assemblies in w consistently remained at baseline given that 'Pause variability' experiments were conducted in the $N_X = 15$ variability condition. In τ_w, also $X \rightarrow X$ was at baseline while $B \rightarrow X$ and $X \rightarrow A$ slightly decreased across pause durations. This was again explained by reduced amounts of cross-sample potentiation due to long pauses.

3.3.3.5 Experiment 'Emphasis': assembly dynamics

In experiment 'Emphasis', τ_w and w showed qualitatively equal dynamics in all synapse assembly types (τ_w: Fig. 3.39 and w: Fig. 3.8). In the 'On' emphasis condition, assembly strengths were consistently stronger than in the 'Off' emphasis condition. These dynamics were explained by increased stimulus firing rates in the 'On' condition and thus, by the increased amount of induced potentiation (Lehfeldt et al. n.d.). Only X largely remained constant across emphasis conditions (τ_w: Fig. 3.39**E** and w: Fig. 3.7**E**). This consistency was explained by the fact that X was independent from emphasis, given that only the grammatical A and B element encoding neural subgroups received increased stimulus firing rates (Lehfeldt et al. n.d.).

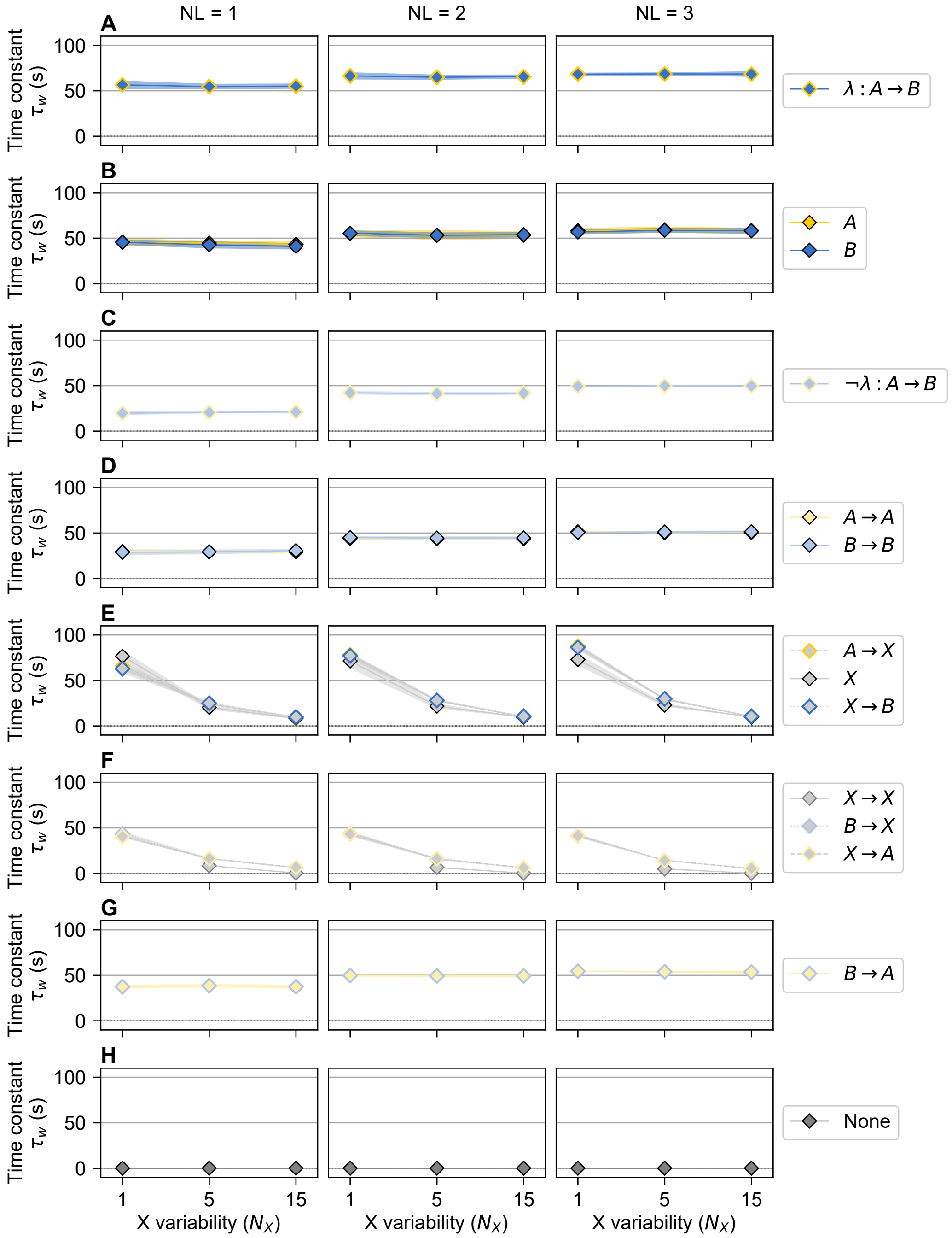


Figure 3.36: Assembly medians (synaptic weight time constant τ_w) in experiment 'X variability'. Each individual data point (= n) indicates mean ± standard deviation (SD) across the RNNs (N = 10). Columns indicate grammar (NL = 1: isolated NAD, NL = 2 and NL = 3: nested NADs). N_X = number of available X elements. Dotted line = lower weight boundary. **A** Grammatical A to B transitions (n = 10). **B** A and B elements (n = 10). **C** Non-grammatical A to B transitions (n = 10). **D** A to A and B to B transitions ($\widehat{AA}\widehat{BB}$, n = 10). **E** X elements, A to X and X to B transitions (χ, n = 10). **F** X to X, B to X and X to A transitions (χ', n = 10). **G** B to A transitions (n = 10). **H** Non-assembly synapses (None, n = 10).

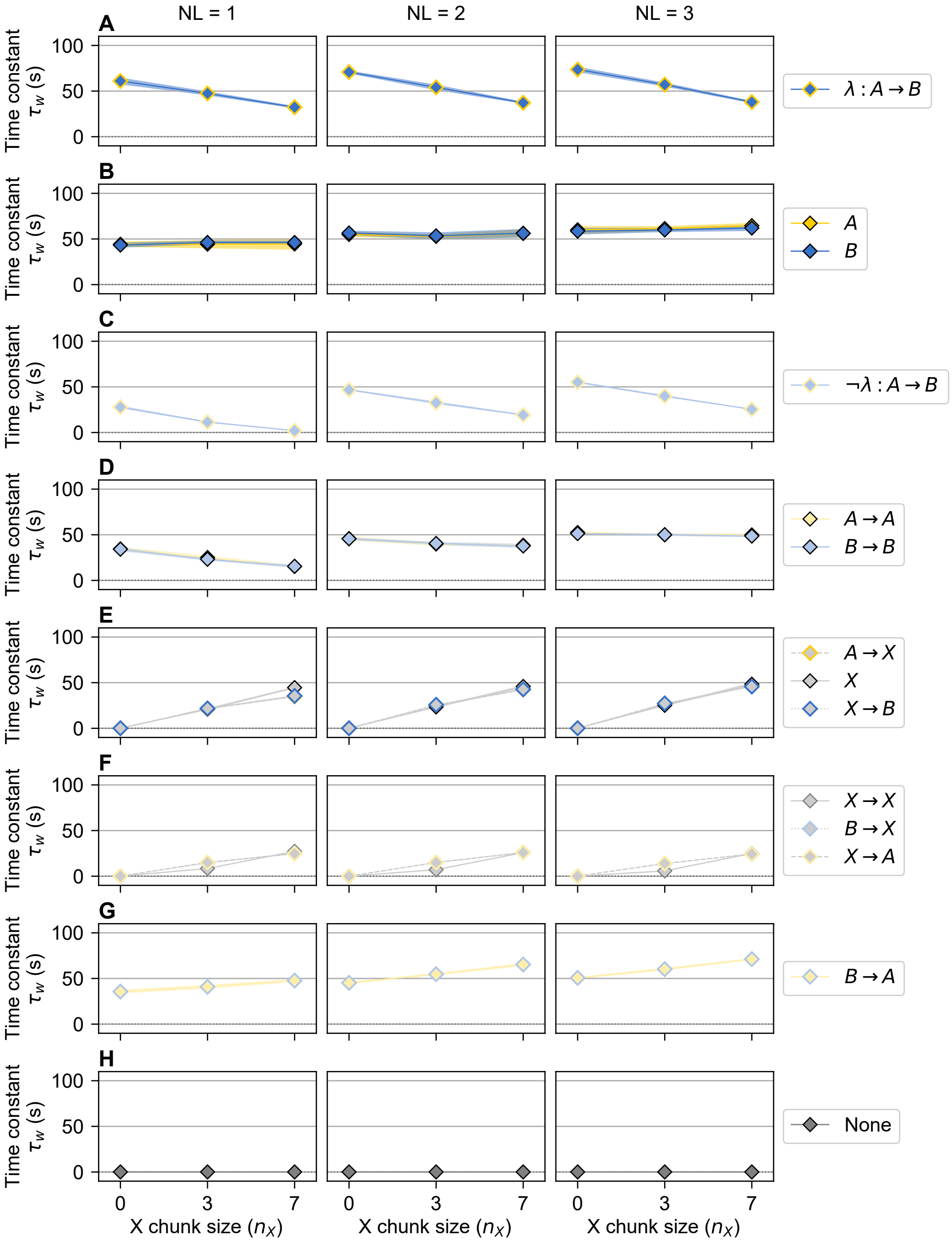


Figure 3.37: Assembly medians (synaptic weight time constant τ_w) in experiment 'X chunk size'. Each individual data point (= n) indicates mean ± standard deviation (SD) across the RNNs (N = 10). Columns indicate grammar (NL = 1: isolated NAD, NL = 2 and NL = 3: nested NADs). N_X = number of available X elements. Dotted line = lower weight boundary. **A** Grammatical A to B transitions (n = 10). **B** A and B elements (n = 10). **C** Non-grammatical A to B transitions (n = 10). **D** A to A and B to B transitions ($\widehat{AA}\widehat{BB}$, n = 10). **E** X elements, A to X and X to B transitions (χ, n = 10). **F** X to X, B to X and X to A transitions (χ', n = 10). **G** B to A transitions (n = 10). **H** Non-assembly synapses (None, n = 10).

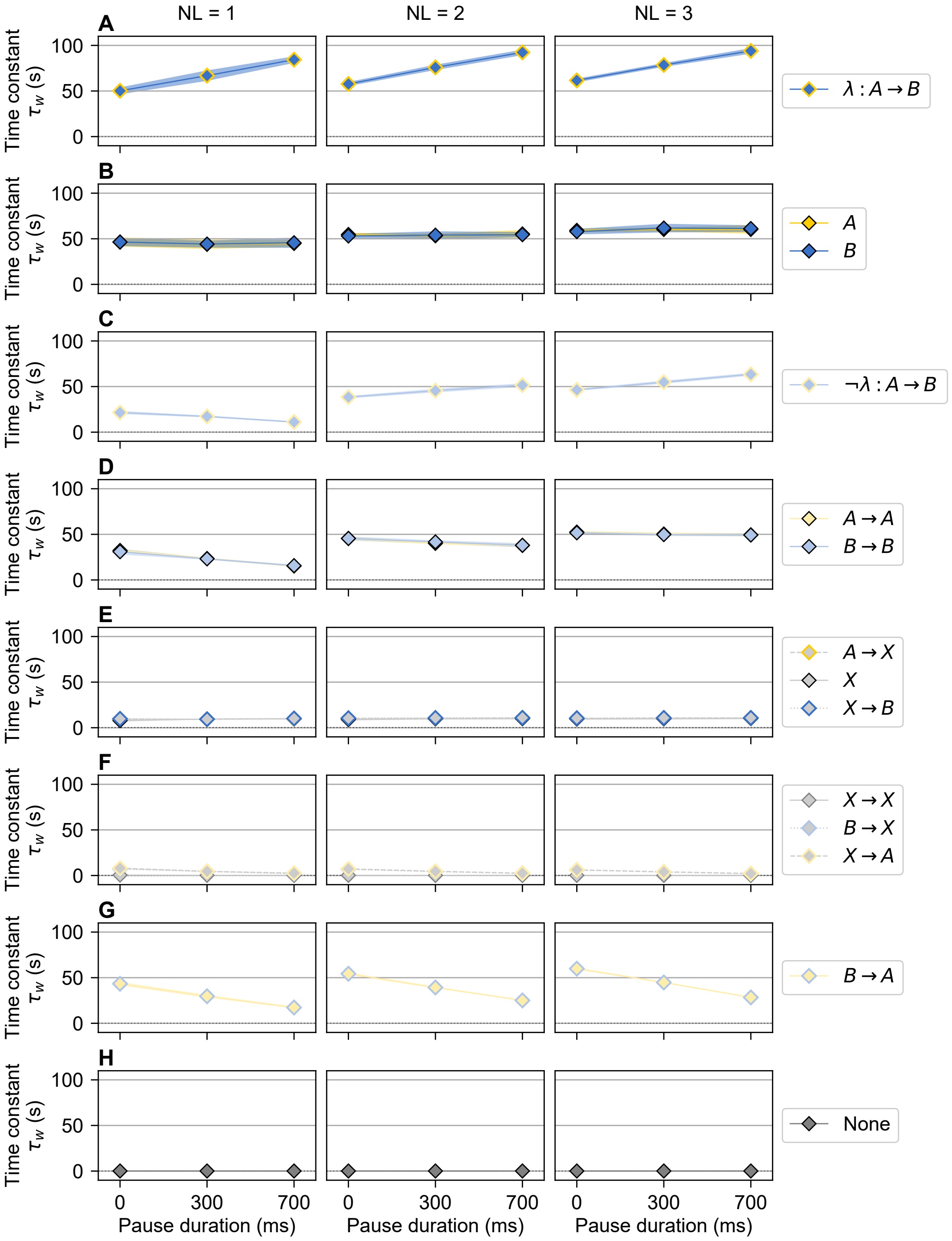


Figure 3.38: Assembly medians (synaptic weight time constant τ_w) in experiment 'Pause variability'. Each individual data point (= n) indicates mean ± standard deviation (SD) across the RNNs (N = 10). Columns indicate grammar (NL = 1: isolated NAD, NL = 2 and NL = 3: nested NADs). N_X = number of available X elements. Dotted line = lower weight boundary. **A** Grammatical A to B transitions (n = 10). **B** A and B elements (n = 10). **C** Non-grammatical A to B transitions (n = 10). **D** A to A and B to B transitions ($\widehat{AA}\widehat{BB}$, n = 10). **E** X elements, A to X and X to B transitions (χ, n = 10). **F** X to X, B to X and X to A transitions (χ', n = 10). **G** B to A transitions (n = 10). **H** Non-assembly synapses (None, n = 10).

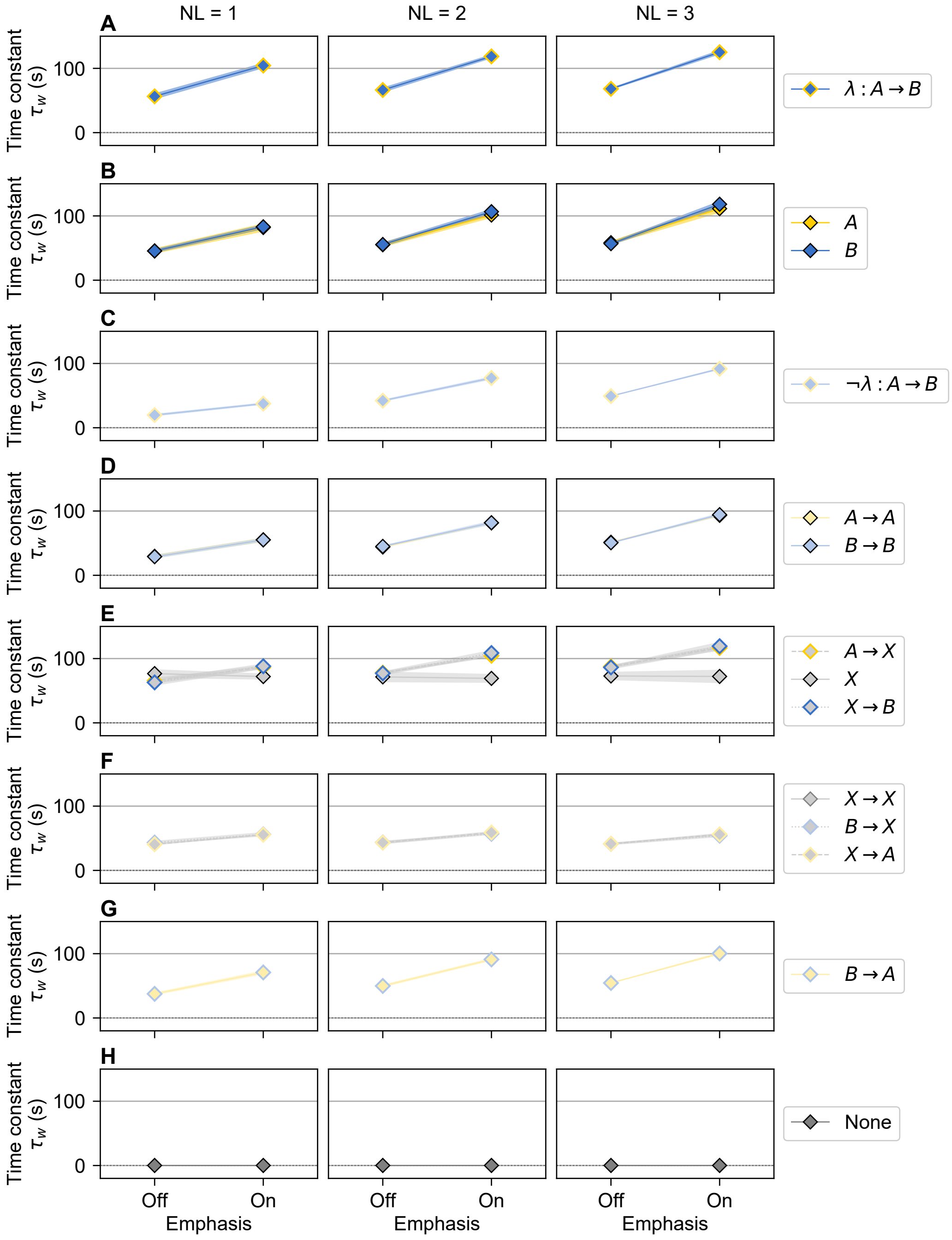


Figure 3.39: Assembly medians (synaptic weight time constant τ_w) in experiment 'Emphasis'. Each individual data point (= n) indicates mean ± standard deviation (SD) across the RNNs (N = 10). Columns indicate grammar (NL = 1: isolated NAD, NL = 2 and NL = 3: nested NADs). N_X = number of available X elements. Dotted line = lower weight boundary. **A** Grammatical A to B transitions (n = 10). **B** A and B elements (n = 10). **C** Non-grammatical A to B transitions (n = 10). **D** A to A and B to B transitions ($\widehat{AA}\widehat{BB}$, n = 10). **E** X elements, A to X and X to B transitions (χ, n = 10). **F** X to X, B to X and X to A transitions (χ', n = 10). **G** B to A transitions (n = 10). **H** Non-assembly synapses (None, n = 10).

3.3.4 Separability measures

3.3.4.1 Complete collection of separability measures and meta analysis

Next to the investigation of synaptic w and τ_w dynamics, the modelled grammar learning performance was further characterised by so called ‘separability measures’. These were defined as the ratios of grammatical (Λ) and non-grammatical ($\neg\Lambda$) synapse assemblies, i.e. $\frac{\Lambda}{\neg\Lambda}$. For details, see Sec. 3.1.2 ‘Separability measures’ (Lehfeldt et al. n.d.). The manuscript by Lehfeldt et al. (n.d.) showed $\frac{\lambda:A\rightarrow B}{\neg\lambda:A\rightarrow B}$ and $\frac{\lambda:A\rightarrow B}{\chi}$ as the selection of separability measures that demonstrated an accordance between modelled and human NAD learning performances. For completeness, the appendix of this thesis included the full set of separability measures across experiments (‘X variability’: Fig. A.1 and Fig. A.2, ‘X chunk size’: Fig. A.3 and Fig. A.4, ‘Pause variability’: Fig. A.5 and Fig. A.6, ‘Emphasis’: Fig. A.7 and Fig. A.8). In Lehfeldt et al. (n.d.), the analysis was focused on separability measures taking the grammatical A to B transition assemblies as a reference. This was motivated by the fact that $\lambda : A \rightarrow B$ was the model equivalent to the grammatical dependency that participants are usually tested for in psycho- and neurolinguistic experiments (Mueller et al. 2012; Winkler et al. 2018a; Wilson et al. 2018). However, next to $\lambda : A \rightarrow B$, the correct acquisition of grammatical A and B elements was as well important for demonstrating an overall successful grammar learning. Thus, also the separability measures taking A and B as references were demonstrated in the appendix of this thesis. Interested readers might take a closer look at the details of all separability measure dynamics (Fig. A.1 to Fig. A.8). However, in order to gain a full view on the grammar learning performance, a meta analysis of the complete set of separability measures was performed (Fig. 3.40 to Fig. 3.47). This analysis indicated whether ratios were above the critical mark of one or below, i.e. provided a binary measure of learning success. Investigating all possible separability measures was of particular importance for demonstrating the general reliability of the learning outcome, whereby ideally all $\frac{\Lambda}{\neg\Lambda}$ ratios resulted in values larger than one. For analysis, the mean values of separability measures minus the respective standard deviations across RNNs (N = 10) were used. This subtraction from the means was done in order to obtain a success measure that also considered the standard deviations of values.

3.3.4.2 Experiment ‘X variability’: meta analysis

In experiment ‘X variability’, separability measures with $\lambda : A \rightarrow B$ as a reference showed equal success distributions in w and τ_w (Fig. 3.40**A** and Fig. 3.41**A**). For both variables, learning was successful in all measures and conditions except the N_X = 1 variability condition. Further, the $\frac{\lambda:A\rightarrow B}{X\rightarrow X}$ separability was NaN in this variability condition given that during training with only one available X element, no X to X transitions occurred (this equivalently applied to the $\frac{A}{X\rightarrow X}$ and $\frac{B}{X\rightarrow X}$ measures). Separability measures with A and B as references showed overall equal dynamics in w and τ_w, however with some variations (Fig. 3.40**B**,**C** and Fig. 3.41**B**,**C**) Here, different success measures in w and τ_w occurred for the experiment conditions NL = 1: $\frac{A}{X\rightarrow A}$ with $N_X = 1$, NL = 2: $\frac{A}{B\rightarrow A}$ with $N_X = 5$, NL = 1: $\frac{B}{B\rightarrow A}$ with $N_X = 15$ and

NL $= 2$: $\frac{B}{B\to A}$ with $N_X = 5$. However, when investigating the belonging separability measure values, differences occurred for those ratios that were concentrated around the critical mark of one (Fig. A.2). Thus, observed differences in success measures were not considered to reflect a systematic effect but where rather interpreted as a result of data variability in the vicinity of the critical mark. Still, these measures indicated that a separation of grammatical from non-grammatical assemblies was not very pronounced here. Across grammars and X variability conditions, $\frac{A}{\lambda:A\to B}$ and $\frac{B}{\lambda:A\to B}$ were below the critical mark of one, indicating that A and B grammar element representations were weaker than grammatical A to B transition assemblies (Fig. A.2). As a final observation, $\frac{B}{A}$ and $\frac{A}{B}$ were both below the critical mark of one, which seemed odd at first. However, as the belonging separability measures were concentrated around the critical mark of one (Fig. A.2), the subtraction of the respective standard deviations apparently returned unsuccessful measures in both. Taken together, the learning performance across grammars and X variability conditions was the most robust in $\lambda : A \to B$. A and B showed more fluctuations in the learning success and interestingly, they were consistently weaker than $\lambda : A \to B$. However, fluctuations did not concern the separability from χ or χ' in $N_X > 1$ variability conditions, so that the beneficial effect of large X variabilities for NAD learning (Lehfeldt et al. n.d.) was further supported.

3.3.4.3 Experiment 'X chunk size': meta analysis

In experiment 'X chunk size', separability measures with $\lambda : A \to B$ as a reference showed overall equal success distributions in w and τ_w, however with one variation in the experiment condition NL $= 2$: $\frac{\lambda:A\to B}{B\to B}$ with $n_x = 7$ (Fig. 3.42**A** and Fig. 3.43**A**). Despite this, all measures were successful for the $n_X = 0$ chunk size condition, i.e. 'Starting small'. For large X chunks (i.e. with $n_X = 3$ and $n_X = 7$), unsuccessful measures occurred in $\frac{\lambda:A\to B}{A}$ and $\frac{\lambda:A\to B}{B}$, indicating that A and B were slightly or prominently stronger than $\lambda : A \to B$ (Fig. A.3). Further, for the largest X chunk size tested, $\frac{\lambda:A\to B}{\chi}$ was unsuccessful across all grammars. Here, also $\frac{\lambda:A\to B}{\widehat{AA}\widehat{BB}}$ was unsuccessful for nested NADs, except for NL $= 2$: $\frac{\lambda:A\to B}{B\to B}$ in w. Thus, long X chunks added the additional difficulty to separate $\lambda : A \to B$ from non-grammatical $A \to A$ and $B \to B$ transitions in nested NADs. Separability measures with A and B as references showed equal success dynamics in w and τ_w, however with one exception for $\frac{A}{\lambda:A\to B}$ in the NL $= 3$ and $n_X = 3$ condition (Fig. 3.42**B**,**C** and Fig. 3.43**B**,**C**). This deviation and also the unsuccessful $\frac{B}{A}$ and $\frac{A}{B}$ measures were, however, again explained by a concentration of the belonging separability measures around the critical mark of one (Fig. A.4). For X chunks with $n_X > 0$, $\frac{A}{B\to A}$ and $\frac{B}{B\to A}$ were unsuccessful, though with an exception for $\frac{B}{B\to A}$ in the NL $= 1$ and $n_X = 3$ condition. Thus, in overall, long X chunks added the additional difficulty to separate A and B from non-grammatical and cross-sample $B \to A$ transitions. Further, $\frac{A}{X}$ and $\frac{B}{X}$ were not successful in the experiment condition NL $= 1$ and $n_X = 7$, though see Fig. A.4. With regard to $\frac{A}{\lambda:A\to B}$ and $\frac{B}{\lambda:A\to B}$, long X chunks were however beneficial. Here, only in the $n_X = 7$ chunk size condition, $\frac{A}{\lambda:A\to B}$ and $\frac{B}{\lambda:A\to B}$ were successful throughout. Finally, $\frac{B}{\neg\lambda:A\to B}$ was not successful in the NL $= 3$ and $n_X = 0$ chunk size condition, though see Fig. A.4. As a final observation, A and B

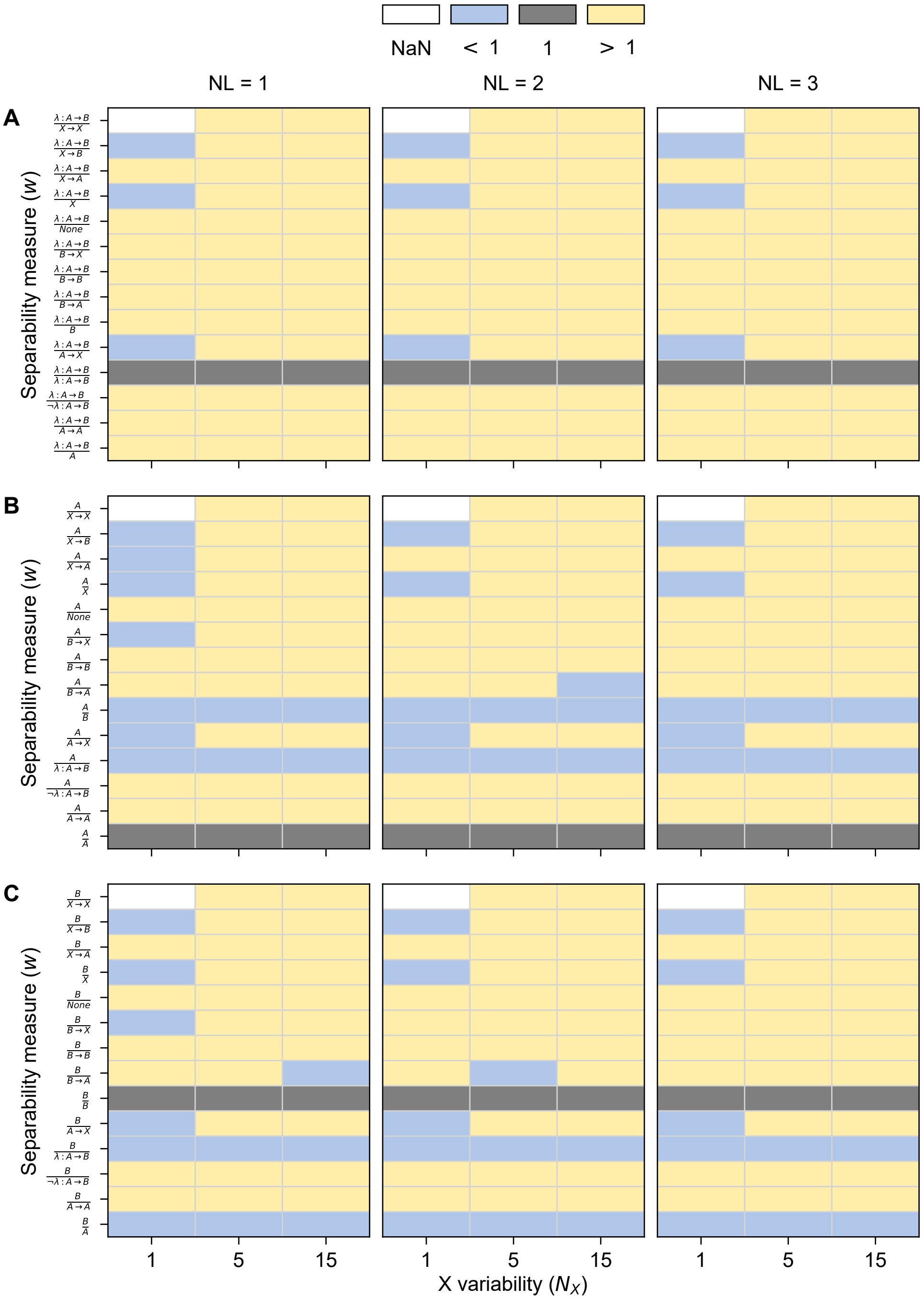


Figure 3.40: Separability measure meta analysis of w in experiment 'X variability'. Each individual tile indicates by colour if the respective separability measure was NaN (white), below one (blue), equal to one (grey) or above one (yellow). **A** Reference assembly: grammatical A to B transitions ($\lambda : A \rightarrow B$). **B** Reference assembly: grammatical A elements (A). **C** Reference assembly: grammatical B elements (B).

were more robust against large X chunks than $\lambda : A \rightarrow B$, as indicated by largely successful $\frac{A}{X}$ and $\frac{B}{X}$ measures across n_X conditions. Taken together, large X chunk

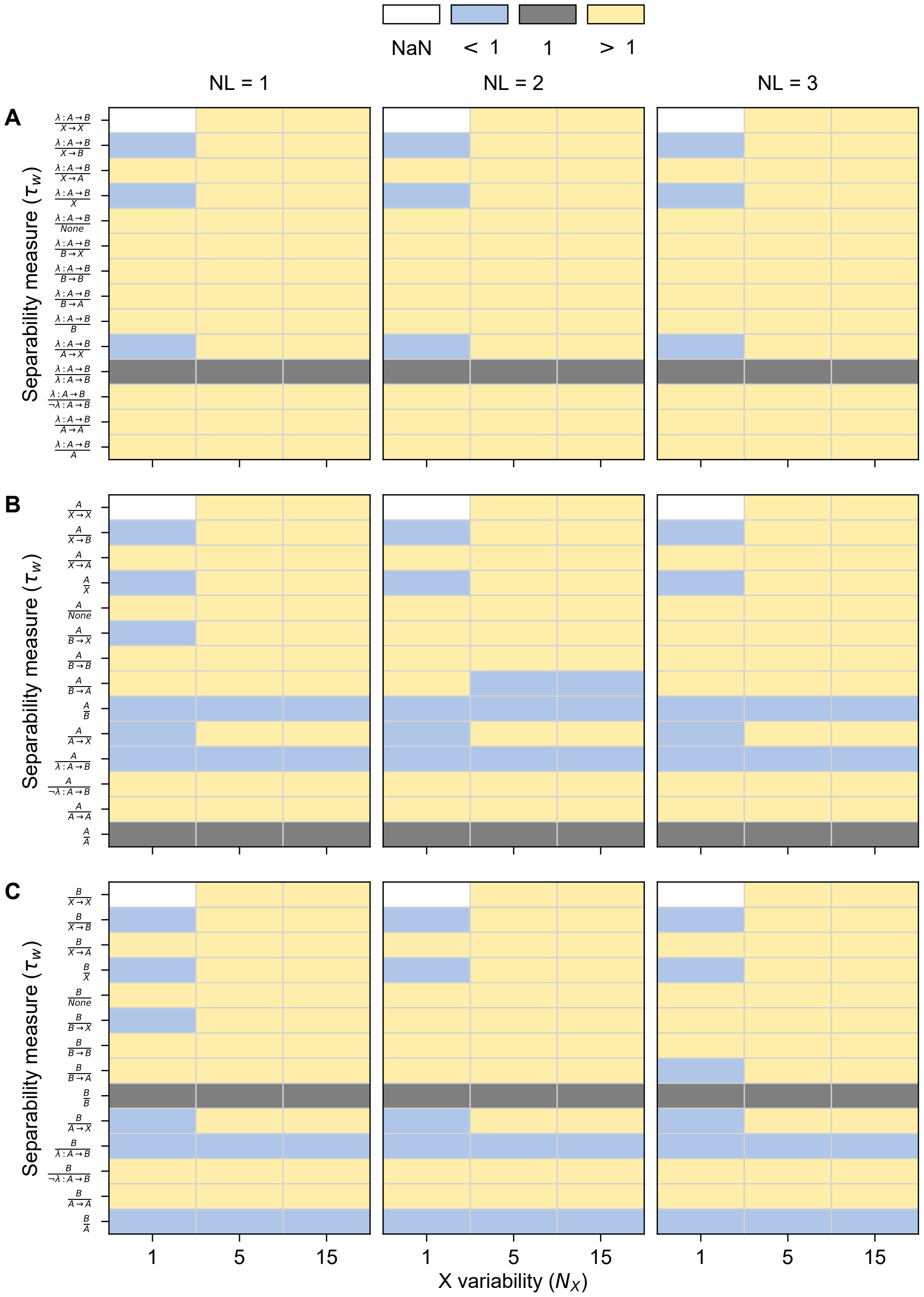


Figure 3.41: Separability measure meta analysis of τ_w in experiment 'X variability'. Each individual tile indicates by colour if the respective separability measure was NaN (white), below one (blue), equal to one (grey) or above one (yellow). **A** Reference assembly: grammatical A to B transitions ($\lambda : A \to B$). **B** Reference assembly: grammatical A elements (A). **C** Reference assembly: grammatical B elements (B).

sizes introduced additional difficulties for the separation from $\widehat{AA}\widehat{BB}$ and $B \to A$. Thus, the beneficial effect of 'Starting small' for NAD learning (Lehfeldt et al. n.d.) was further supported.

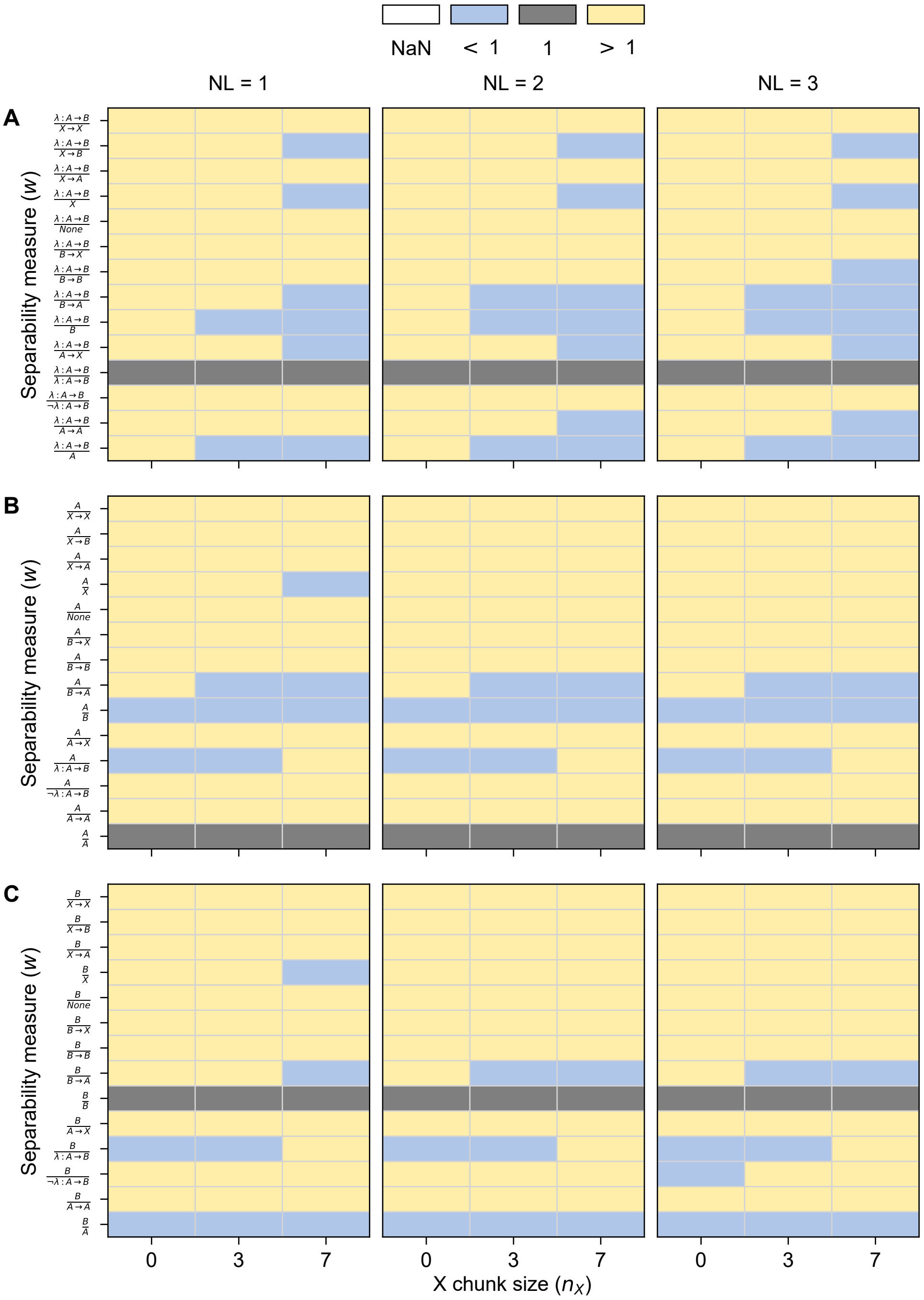


Figure 3.42: Separability measure meta analysis of w in experiment 'X chunk size'. Each individual tile indicates by colour if the respective separability measure was NaN (white), below one (blue), equal to one (grey) or above one (yellow). **A** Reference assembly: grammatical A to B transitions ($\lambda : A \to B$). **B** Reference assembly: grammatical A elements (A). **C** Reference assembly: grammatical B elements (B).

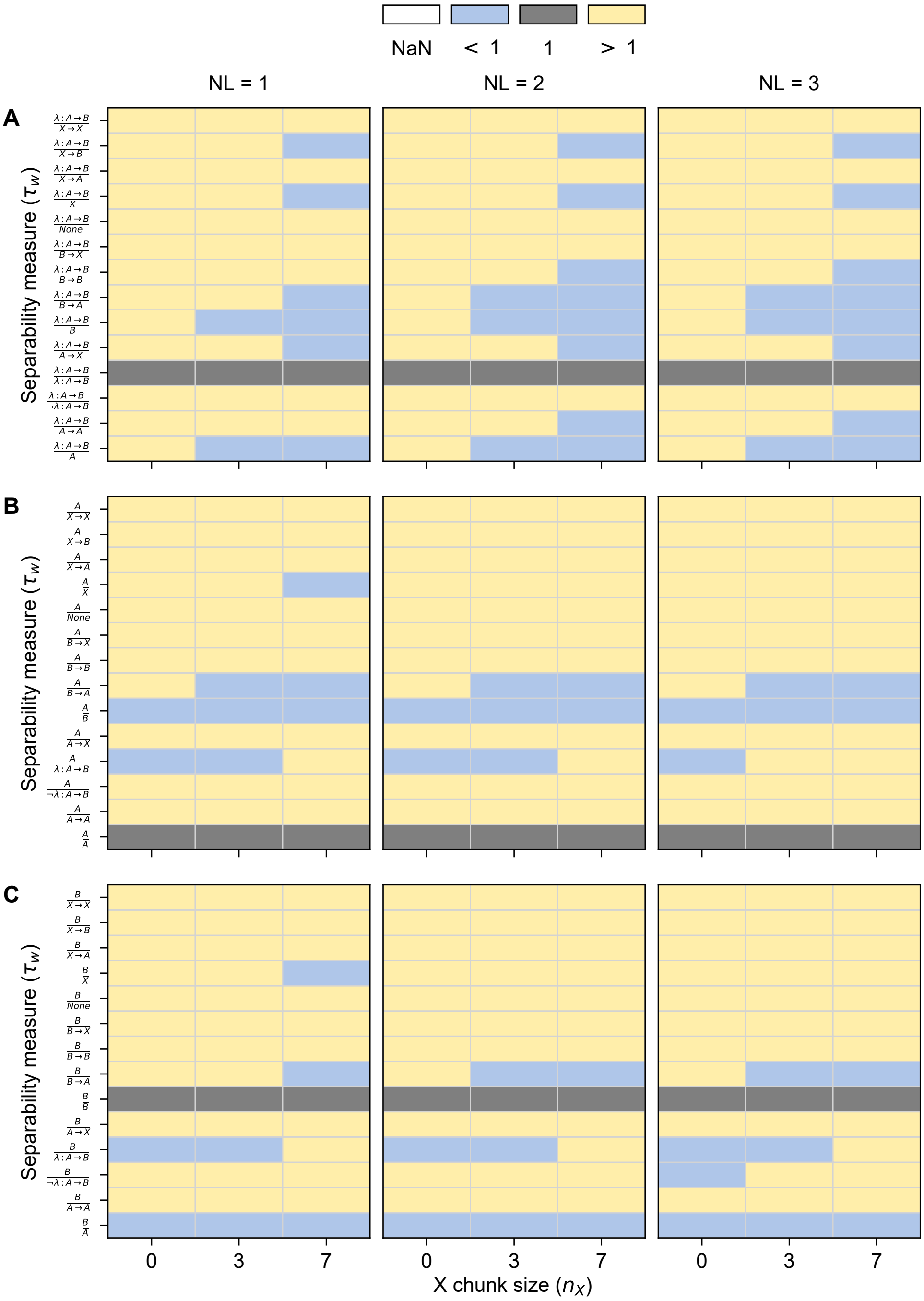


Figure 3.43: Separability measure meta analysis of τ_w in experiment 'X chunk size'. Each individual tile indicates by colour if the respective separability measure was NaN (white), below one (blue), equal to one (grey) or above one (yellow). **A** Reference assembly: grammatical A to B transitions ($\lambda : A \to B$). **B** Reference assembly: grammatical A elements (A). **C** Reference assembly: grammatical B elements (B).

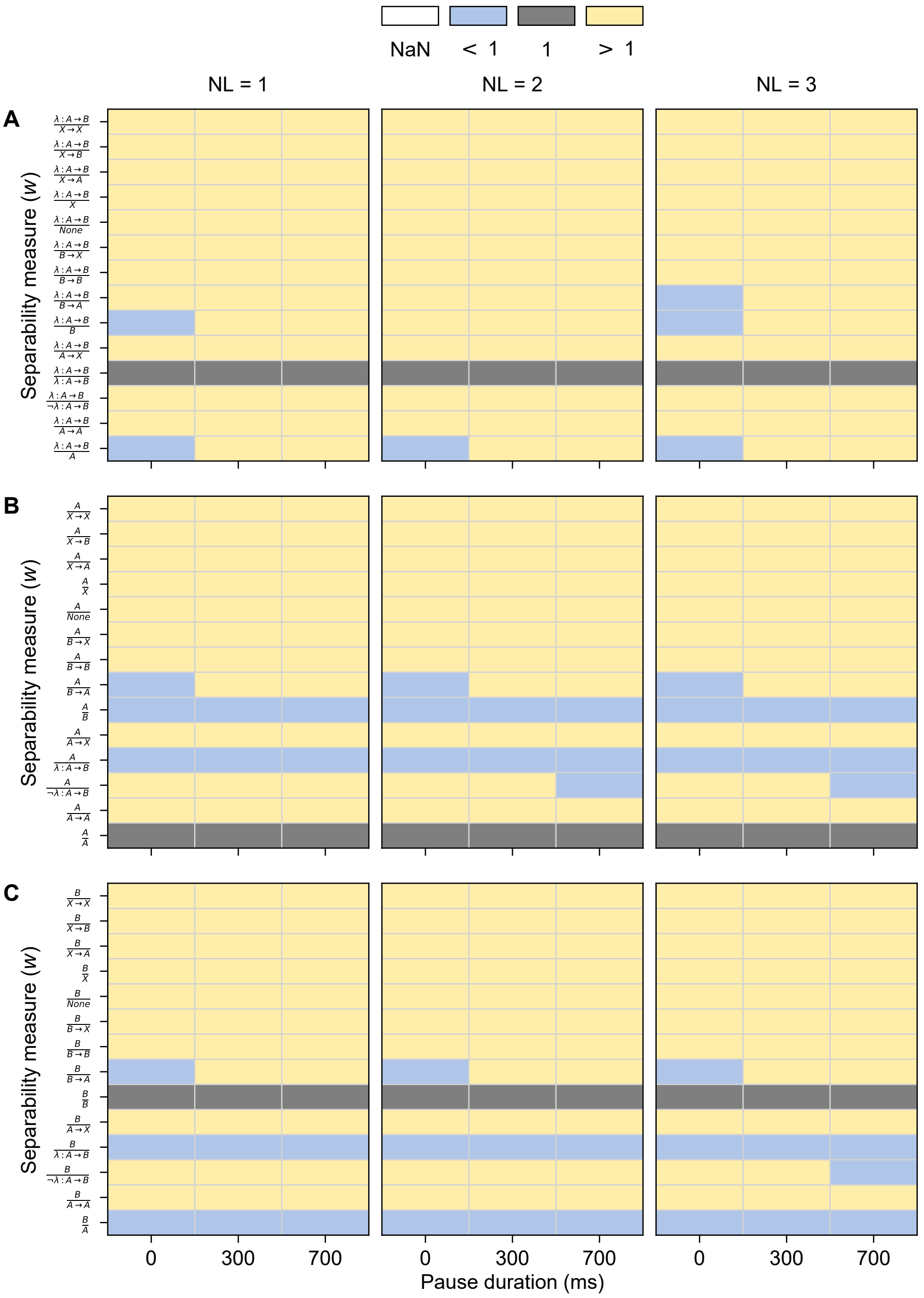


Figure 3.44: Separability measure meta analysis of w in experiment 'Pause variability'. Each individual tile indicates by colour if the respective separability measure was NaN (white), below one (blue), equal to one (grey) or above one (yellow). **A** Reference assembly: grammatical A to B transitions ($\lambda : A \rightarrow B$). **B** Reference assembly: grammatical A elements (A). **C** Reference assembly: grammatical B elements (B).

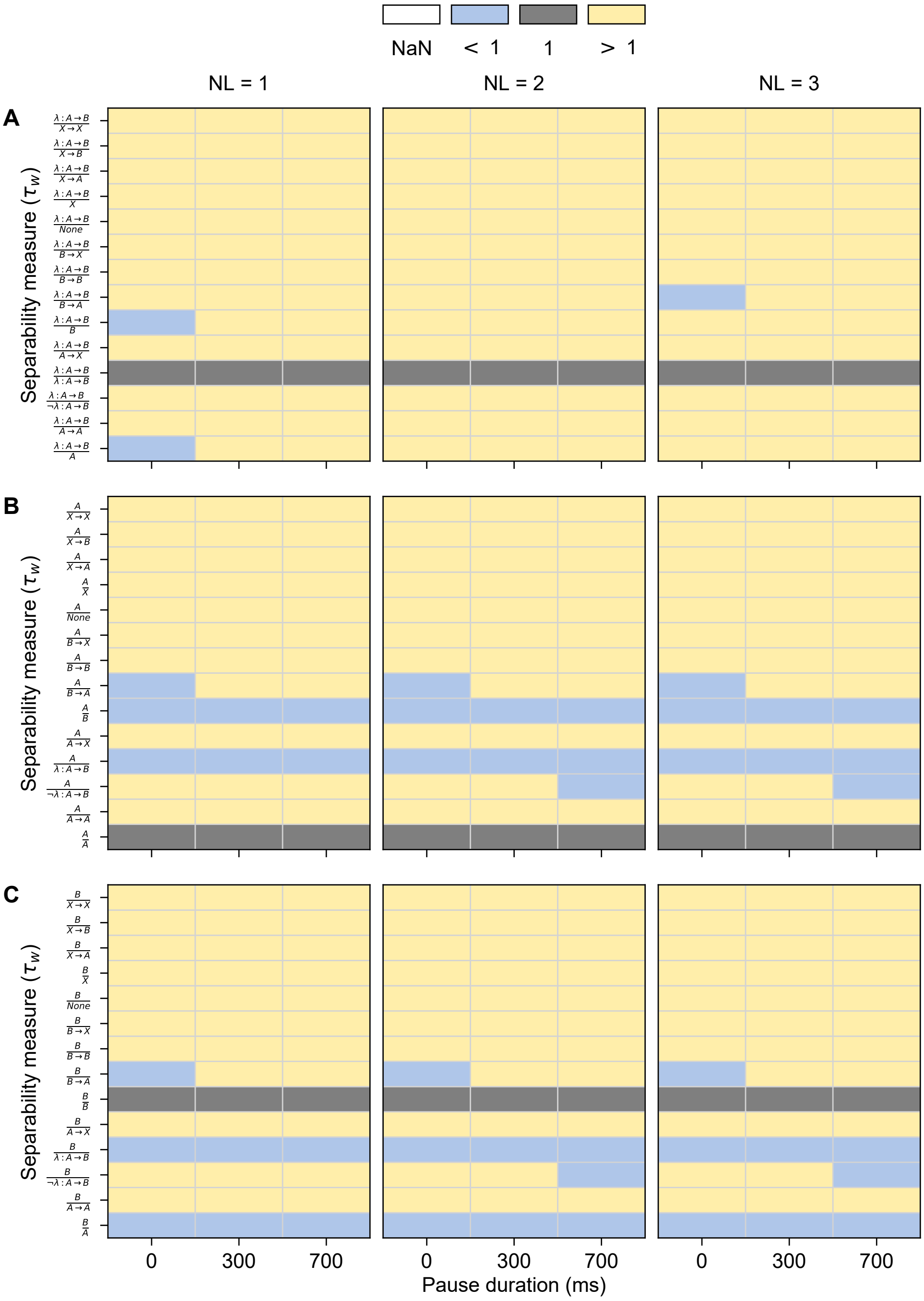


Figure 3.45: Separability measure meta analysis of τ_w in experiment 'Pause variability'. Each individual tile indicates by colour if the respective separability measure was NaN (white), below one (blue), equal to one (grey) or above one (yellow). **A** Reference assembly: grammatical A to B transitions ($\lambda : A \rightarrow B$). **B** Reference assembly: grammatical A elements (A). **C** Reference assembly: grammatical B elements (B).

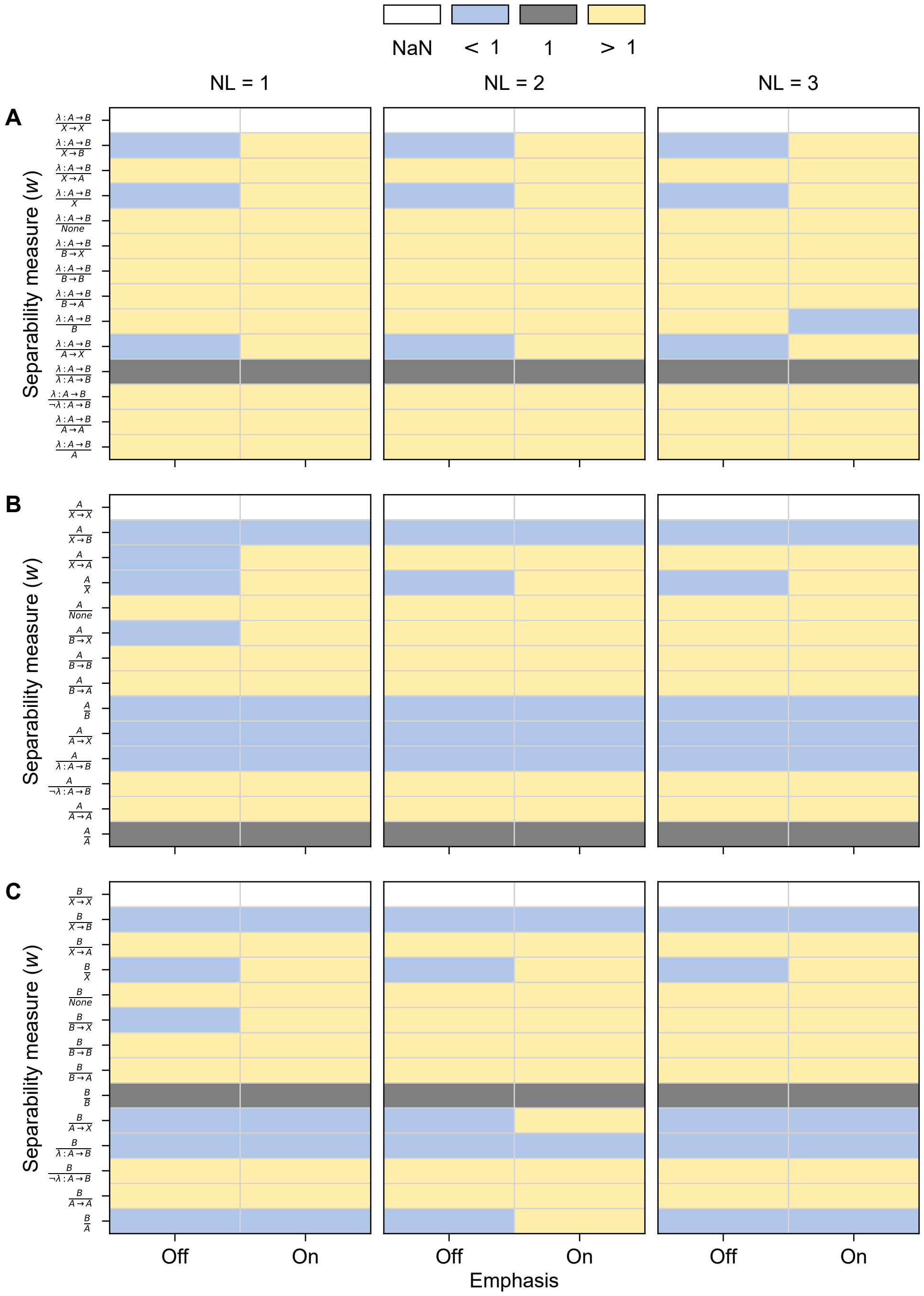


Figure 3.46: Separability measure meta analysis of w in experiment 'Emphasis'. Each individual tile indicates by colour if the respective separability measure was NaN (white), below one (blue), equal to one (grey) or above one (yellow). **A** Reference assembly: grammatical A to B transitions ($\lambda : A \rightarrow B$). **B** Reference assembly: grammatical A elements (A). **C** Reference assembly: grammatical B elements (B).

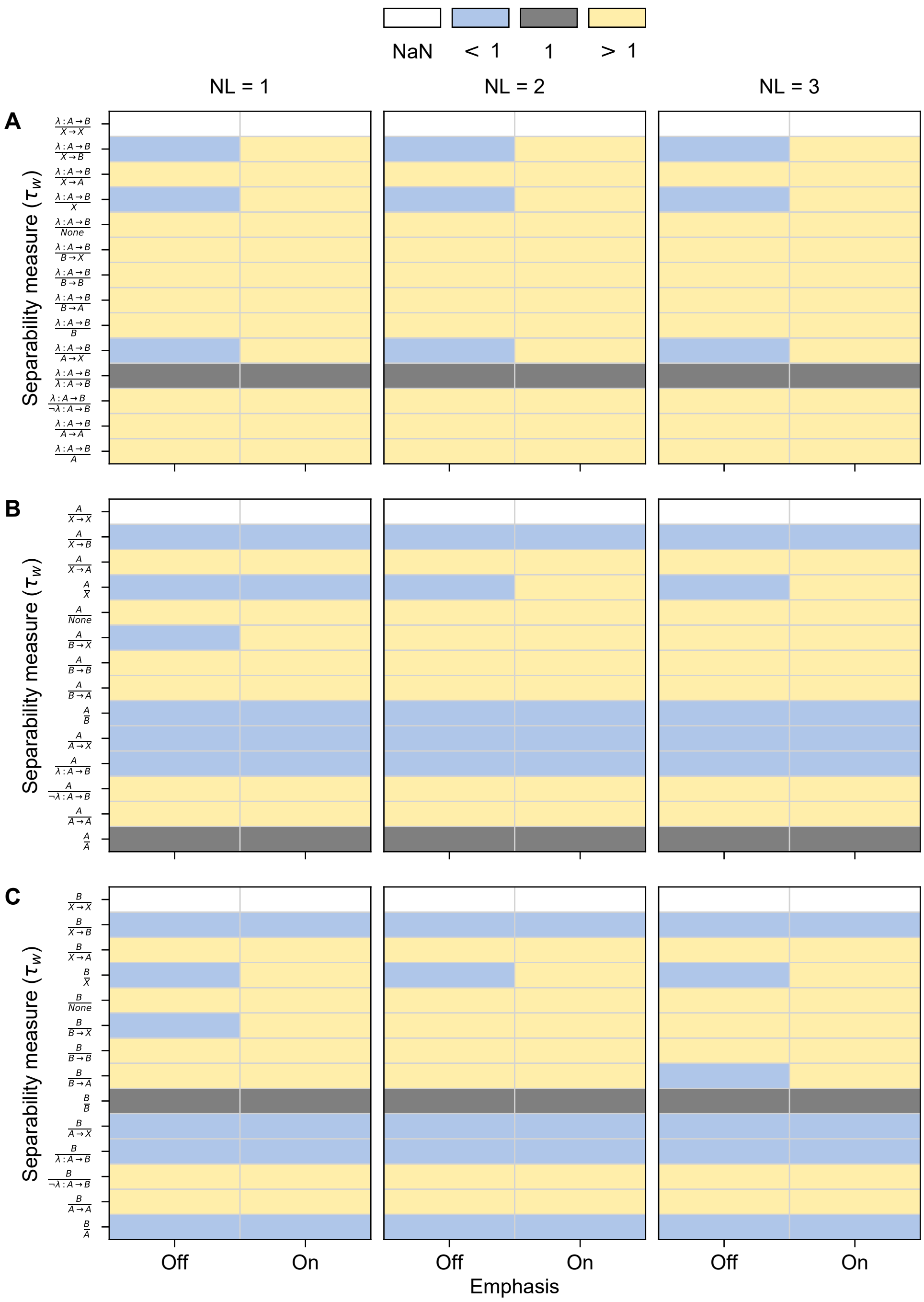


Figure 3.47: Separability measure meta analysis of τ_w in experiment 'Emphasis'. Each individual tile indicates by colour if the respective separability measure was NaN (white), below one (blue), equal to one (grey) or above one (yellow). **A** Reference assembly: grammatical A to B transitions ($\lambda : A \to B$). **B** Reference assembly: grammatical A elements (A). **C** Reference assembly: grammatical B elements (B).

3.3.4.4 Experiment 'Pause variability': meta analysis

In experiment 'Pause variability', separability measures with $\lambda : A \rightarrow B$ as a reference showed overall equal success distributions in w and τ_w, however with some variations (Fig. 3.44**A** and Fig. 3.45**A**). Here, different success measures in w and τ_w occurred for the experiment conditions NL = 2: $\frac{\lambda:A\rightarrow B}{A}$ with $\cup_\Delta = 0$ ms, NL = 3: $\frac{\lambda:A\rightarrow B}{A}$ with $\cup_\Delta = 0$ ms and NL = 3: $\frac{\lambda:A\rightarrow B}{B}$ with $\cup_\Delta = 0$ ms. Throughout, unsuccessful measures only occurred during training without stimulus pauses, i.e. in the $\cup_\Delta = 0$ ms condition. Separability measures with A and B as references showed overall equal success dynamics in w and τ_w, however with one exception for $\frac{B}{\neg\lambda:A\rightarrow B}$ in the NL = 2 and $\cup_\Delta = 700$ ms condition (Fig. 3.44**B**,**C** and Fig. 3.45**B**,**C**). The separation from χ and χ' was successful across all pause conditions. However, in the $\cup_\Delta = 0$ ms condition, $\frac{A}{B\rightarrow A}$ and $\frac{B}{B\rightarrow A}$ were not successful. Further, in nested NADs, $\frac{A}{\neg\lambda:A\rightarrow B}$ and $\frac{B}{\neg\lambda:A\rightarrow B}$ were largely not successful during training with the longest pause duration tested, i.e. $\cup_\Delta = 700$ ms. Again, $\frac{B}{A}$ and $\frac{A}{B}$ were consistently both below the critical mark of one, though see Fig. A.6. Finally, also $\frac{A}{\lambda:A\rightarrow B}$ and $\frac{B}{\lambda:A\rightarrow B}$ were consistently unsuccessful, indicating that $\lambda : A \rightarrow B$ was slightly or prominently stronger than A and B (Fig. A.6). Taken together, the beneficial effect of long stimulus pauses for NAD learning (Lehfeldt et al. n.d.) was further supported. However, in nested NADs, the separability of A and B from $\neg\lambda : A \rightarrow B$ suffered from pause conditions $\cup_\Delta > 300$ ms. Thus, the beneficial effect of long stimulus pauses has to be considered within this identified constraint (Fig. A.6).

3.3.4.5 Experiment 'Emphasis': meta analysis

In experiment 'Emphasis', separability measures with $\lambda : A \rightarrow B$ as references showed overall equal success distributions in w and τ_w, however with one exception for the experiment condition NL = 3: $\frac{\lambda:A\rightarrow B}{B}$ with 'On' emphasis (Fig. 3.46**A** and Fig. 3.47**A**), though see Fig. A.7. Despite this, all remaining measures were consistently successful in the 'On' emphasis condition. Separability measures with A and B as references showed overall equal success distributions in w and τ_w, however with exceptions for the experiment conditions NL = 1: $\frac{A}{X\rightarrow A}$ with 'Off' emphasis, NL = 1: $\frac{A}{X}$ with 'On' emphasis, NL = 2: $\frac{B}{A\rightarrow X}$ with 'On' emphasis, NL = 2: $\frac{B}{A}$ with 'On' emphasis and NL = 3: $\frac{B}{B\rightarrow A}$ with 'Off' emphasis (Fig. 3.46**B**,**C** and Fig. 3.47**B**,**C**), though see Fig. A.8. However, the separability measures $\frac{A}{A\rightarrow X}$, $\frac{B}{A\rightarrow X}$ and $\frac{A}{X\rightarrow B}$, $\frac{B}{X\rightarrow B}$ remained largely unsuccessful in the 'On' emphasis condition. Thus, in contrast to $\lambda : A \rightarrow B$, the separability of A and B from χ did not increase consistently by emphasis. Again, $\frac{B}{A}$ and $\frac{A}{B}$ were largely both below the critical mark of one, though see Fig. A.8. Throughout, $\frac{\lambda:A\rightarrow B}{X\rightarrow X}$, $\frac{A}{X\rightarrow X}$ and $\frac{B}{X\rightarrow X}$ were NaN, given that training was conducted in the $N_X = 1$ variability condition. Finally, also $\frac{A}{\lambda:A\rightarrow B}$ and $\frac{B}{\lambda:A\rightarrow B}$ were consistently unsuccessful, indicating that $\lambda : A \rightarrow B$ was slightly stronger than A and B across the emphasis conditions (Fig. A.8). Taken together, the beneficial effect of emphasis on the $\frac{\lambda:A\rightarrow B}{X}$ separability (Lehfeldt et al. n.d.) was largely also present in $\frac{A}{X}$ and $\frac{B}{X}$. However, as only the separability measure $\frac{\lambda:A\rightarrow B}{\chi}$ consistently benefited from emphasis, its facilitating effect has to be considered within the here identified constraints.

3.3.5 SLMT for robust learning

A major problem in the research area of spike-based statistical learning is the emergence of unstable network states, also referred to as ‘runaway activity’ (Abbott and Nelson 2000; Gütig et al. 2003; Chistiakova et al. 2014; Chistiakova et al. 2015; Keck et al. 2017). Runaway states are characterised by strong ‘on-off’ oscillations at maximal firing rates (Lazar et al. 2009; Zenke et al. 2013; Litwin-Kumar and Doiron 2014) and by saturated synaptic weights (Chen et al. 2013). As a consequence, networks are prevented from proper functioning and previously established synaptic memories are destroyed. Underlying to runaway activity is a positive feedback loop introduced by the associativity of spike-based statistical learning (Zenke et al. 2013; Keck et al. 2017). During training, the continuous strengthening of synapses between neurons that share temporally correlated activities leads to continuously stronger excitatory activations and hence, increased neural firing. In turn, this promotes the further growth of synapse strengths and thereby causes an even further increase of spiking activity. At some point, this positive feedback loop becomes so strong that previously silent neurons, i.e. those that were not part of the memory subset, also become activated. Consequently, the growth of synapses external to the actual memory is initiated, adding extra spiking activity and potentiation to the network state. As a final result of this spreading, networks inevitably converge towards unstable runaway dynamics. Solving this issue is still a topic of ongoing research, whereby the main idea for preventing runaway states is to combine purely associative learning with other compensatory plasticity mechanisms (Zenke et al. 2013; Chistiakova et al. 2014; Chistiakova et al. 2015; Keck et al. 2017; Zenke and Gerstner 2017). For example, stability was achieved by extending associative learning with neuronal intrinsic plasticity and normalisation (Lazar et al. 2009), fast rate detectors (Zenke et al. 2013), heterosynaptic plasticity (Chen et al. 2013), a combination of inhibitory plasticity and normalisation (Litwin-Kumar and Doiron 2014), a combination of short-term and inhibitory plasticity with a consolidation mechanism (Zenke et al. 2015) or by using structural plasticity for learning (Gallinaro et al. 2022). Further approaches included additional dynamics of synaptic variables such as bistability (Fusi 2002; Graupner and Brunel 2012a; Graupner and Brunel 2012b) or adaptive weight decays (Zuo et al. 2017a; Zuo et al. 2017b; Panda and Roy 2017; Panda et al. 2018). Here, the idea was that synaptic variables are not temporally infinite but rather exhibit bistable or decaying behaviours during the absence of input at the synapse. Especially weight decay adaptivity was interpreted as a way to implement forgetting and has already been shown to stabilise spike-based learning (Panda and Roy 2017) and to increase performance by preventing catastrophic forgetting (Panda et al. 2018). The concept of forgetting by weight decay recently also found application in models of auditory predictions (Harrison et al. 2020) or statistical sequence learning (Endress and Johnson 2021). In this thesis, stable learning was achieved by a combination of spike-timing dependent plasticity (STDP), neural intrinsic plasticity (IP) and a short- to long-term memory transition (SLMT) mechanism that implemented an activity dependent weight decay adaptivity. For details on the SLMT implementation see Sec. 3.1.2 ‘Spike-timing dependent plasticity (STDP) with short- to long-term memory transition (SLMT)’ (Lehfeldt et al. n.d.). In order to demonstrate the stabilising effect of SLMT, the experiments

'X variability' and 'Emphasis' were run with STDP and IP as only plasticity types, i.e. without SLMT. In response to the same experimental conditions as in the grammar learning experiment series (compare Fig. 3.48 and Fig. 3.4), runaway activities occurred during training without SLMT. While during learning with STDP, IP and SLMT no unstable dynamics were observed (300 simulations in total), during training with STDP and IP only, runaway occurred in 37 out of 120 simulations. In experiment 'X variability', learning of NL = 1 and NL = 2 grammars was still stable while learning of NL = 3 grammars resulted in runaway dynamics (Fig. 3.49). This was demonstrated by saturation of synaptic weights and overall larger standard deviations of weight medians. In experiment 'Emphasis', runaway occurred in NL = 1 and NL = 2 grammars for the 'On' condition and in NL = 3 grammars for both 'Off' and 'On' conditions (Fig. 3.50). Examples of training runs with runaway spiking activity were demonstrated in Fig. 3.51 and Fig. 3.52. Throughout, the stabilising effect of SLMT was explained by the adaptive weight decay, as this constantly counteracted the positive feedback loop induced by associative learning. Due to decaying weights, the unstable spreading of excitatory activation and hence, the neural firing outside of the memory subsets was successfully prevented. Within the training conditions of this thesis, SLMT was therefore sufficient to prevent unstable runaway dynamics.

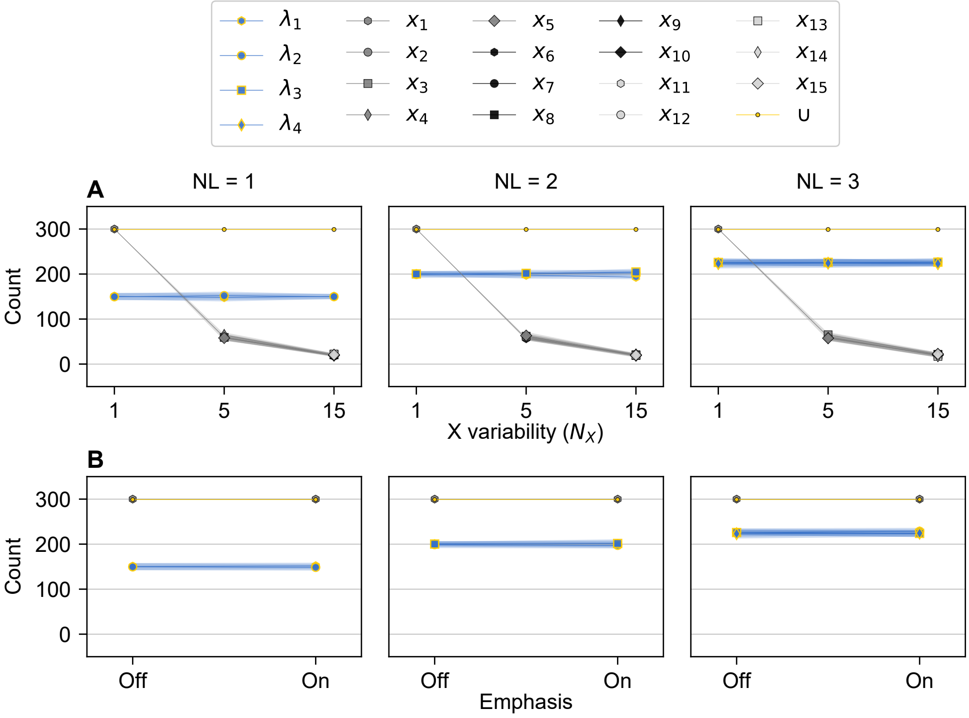


Figure 3.48: Stimulus element counts in all training sequences of experiments without SLMT. Each individual data point (= n) indicates mean count ± standard deviation (SD) of grammatical A and B pairs (λ), non-grammatical X elements (x) and pause elements ($\cup$) across the RNNs (N = 10). **A** Counts in experiment 'X variability' (n = 10); N_X = number of available X elements. **B** Counts in experiment 'Emphasis' (n = 10).

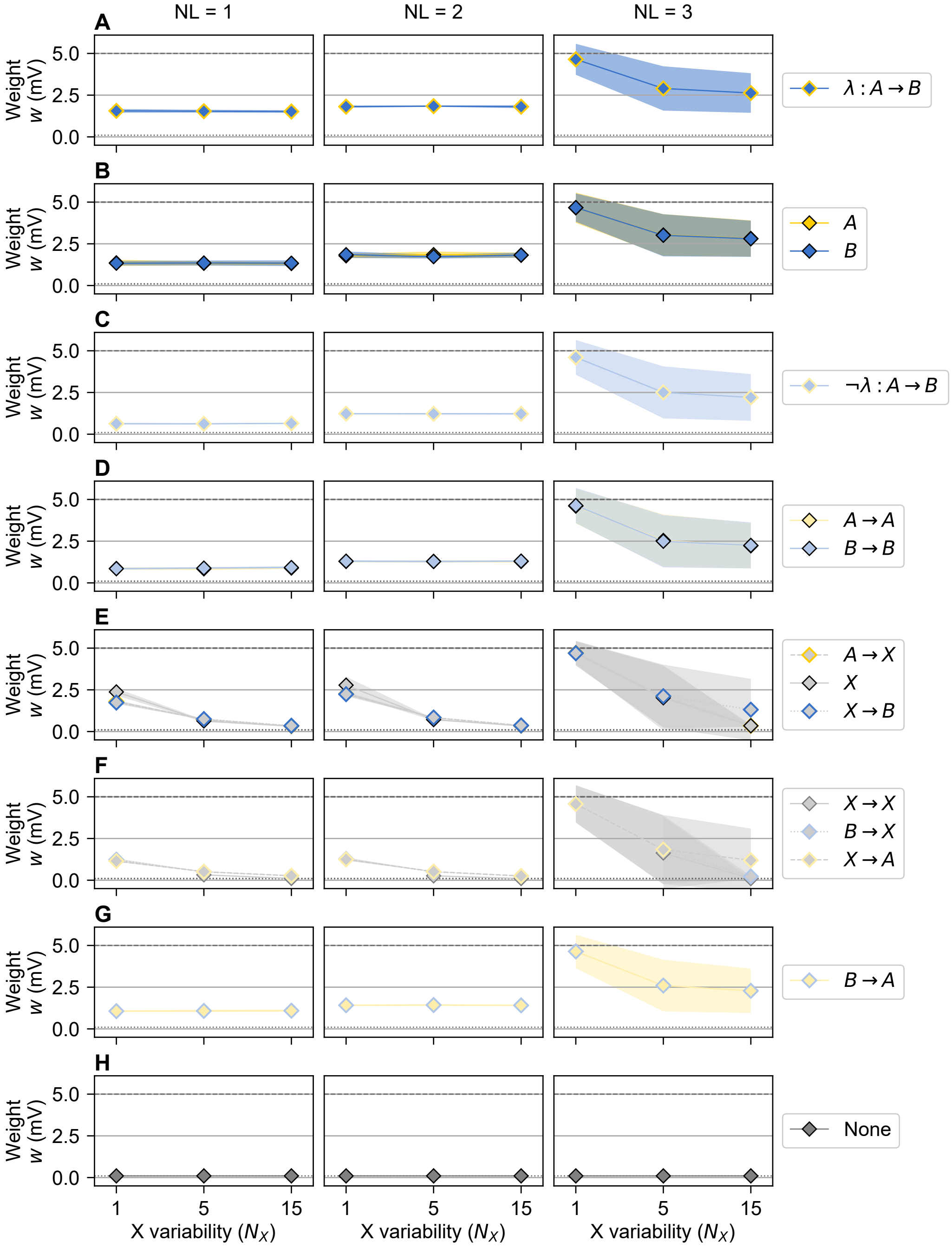


Figure 3.49: Assembly medians (synaptic weight w) in experiment 'X variability' and without SLMT. Each individual data point (= n) indicates mean ± standard deviation (SD) across the RNNs (N = 10). Columns indicate grammar (NL = 1: isolated NAD, NL = 2 and NL = 3: nested NADs). N_X = number of available X elements. Dotted line = lower weight boundary. **A** Grammatical A to B transitions (n = 10). **B** A and B elements (n = 10). **C** Non-grammatical A to B transitions (n = 10). **D** A to A and B to B transitions ($\widehat{AA}\widehat{BB}$, n = 10). **E** X elements, A to X and X to B transitions (χ, n = 10). **F** X to X, B to X and X to A transitions (χ', n = 10). **G** B to A transitions (n = 10). **H** Non-assembly synapses (None, n = 10).

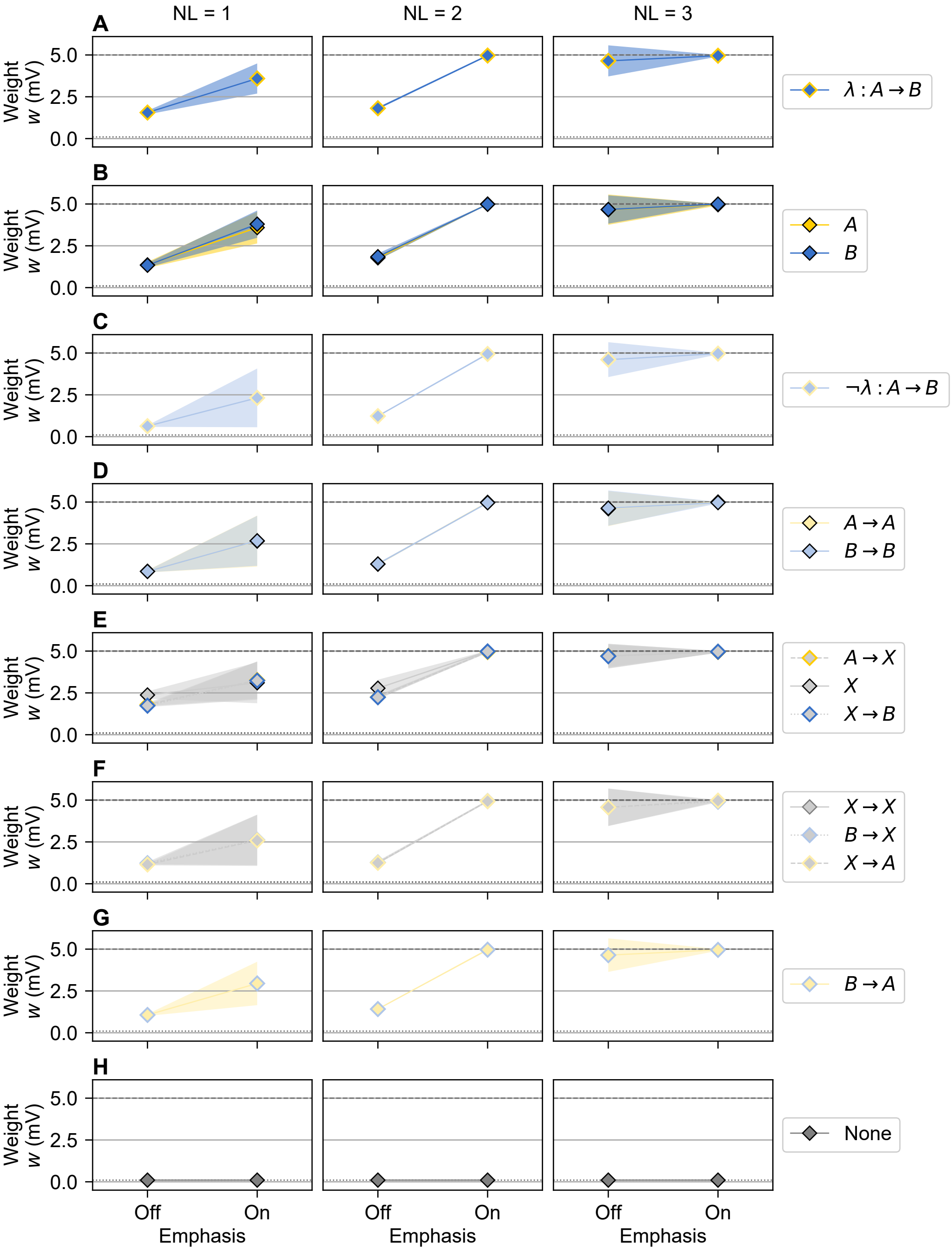


Figure 3.50: Assembly medians (synaptic weight w) in experiment 'Emphasis' and without SLMT. Each individual data point (= n) indicates mean ± standard deviation (SD) across the RNNs (N = 10). Columns indicate grammar (NL = 1: isolated NAD, NL = 2 and NL = 3: nested NADs). N_X = number of available X elements. Dotted line = lower weight boundary. **A** Grammatical A to B transitions (n = 10). **B** A and B elements (n = 10). **C** Non-grammatical A to B transitions (n = 10). **D** A to A and B to B transitions ($\widehat{AA}\widehat{BB}$, n = 10). **E** X elements, A to X and X to B transitions (χ, n = 10). **F** X to X, B to X and X to A transitions (χ', n = 10). **G** B to A transitions (n = 10). **H** Non-assembly synapses (None, n = 10).

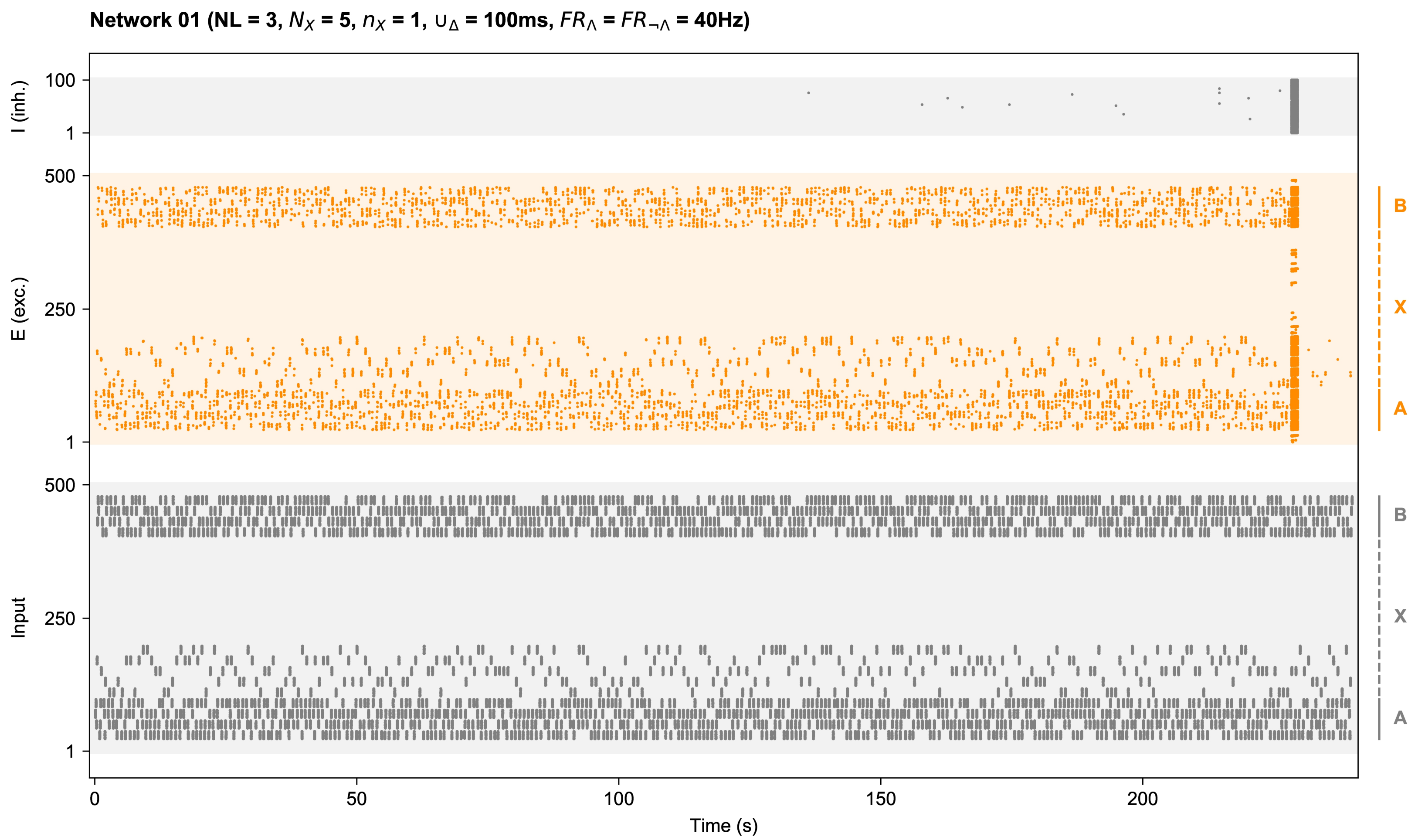


Figure 3.51: Example spiking network activity during training in experiment 'X variability' and without SLMT. NL = nesting level; N_X = number of available X elements; n_X = number of X elements per grammar sample; $\cup_\Delta$ pause duration between grammar samples; FR = Poisson stimulus firing rate; Λ = grammatical neuron subgroups; $\neg\Lambda$ = non-grammatical neuron subgroups; Input = input population; E = excitatory population; I = inhibitory population; A = A element encoding subgroups; X = X element encoding subgroups; B = B element encoding subgroups.

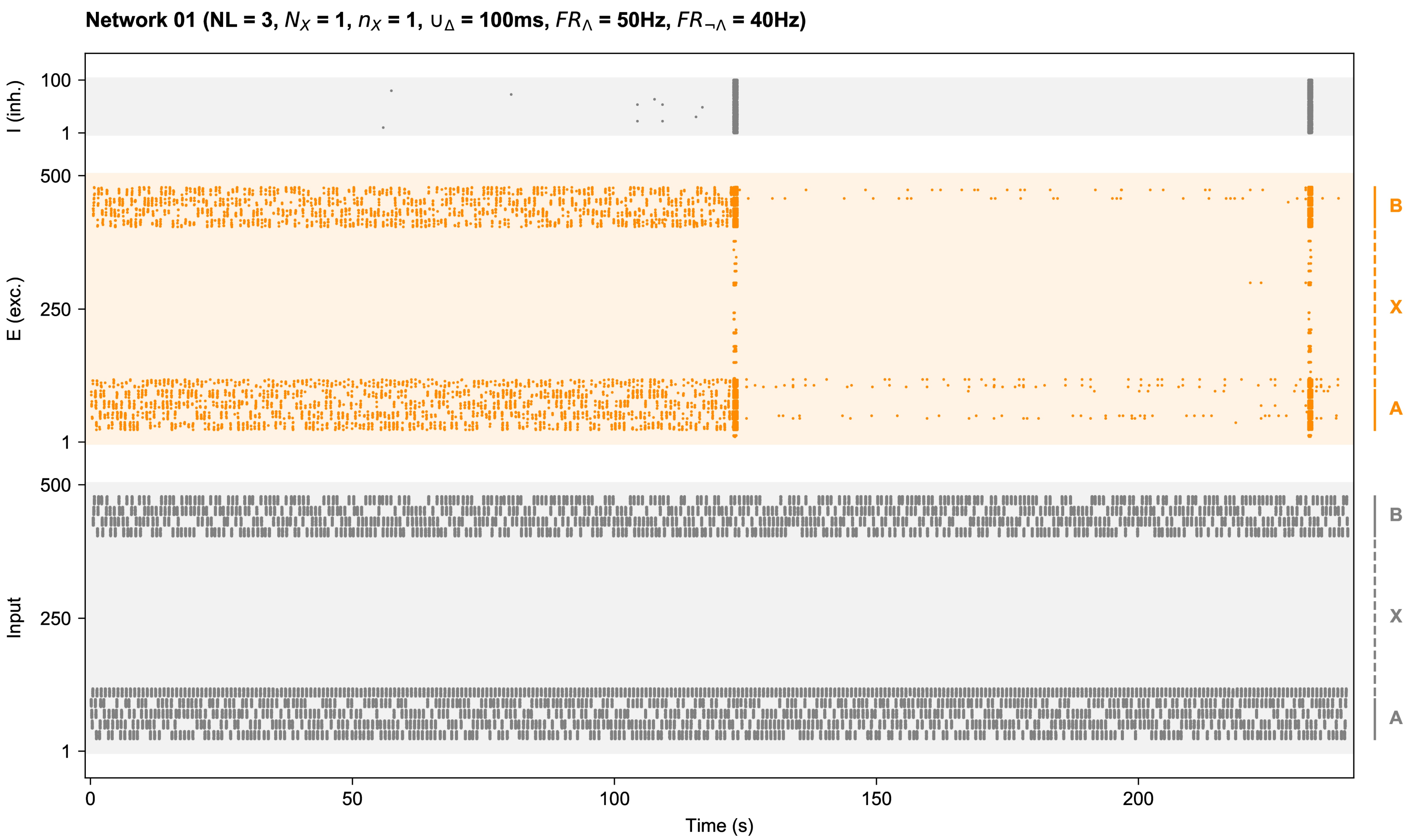


Figure 3.52: Example spiking network activity during training in experiment 'Emphasis' and without SLMT. NL = nesting level; N_X = number of available X elements; n_X = number of X elements per grammar sample; $\cup_\Delta$ pause duration between grammar samples; FR = Poisson stimulus firing rate; Λ = grammatical neuron subgroups; $\neg\Lambda$ = non-grammatical neuron subgroups; Input = input population; E = excitatory population; I = inhibitory population; A = A element encoding subgroups; X = X element encoding subgroups; B = B element encoding subgroups.

Chapter 4

Achievements and future directions

4.1 Overcoming the ‘interface problem’

4.1.1 A link between linguistics and neuroscience

This thesis provided a solution for overcoming the ‘interface problem’ between linguistics and neuroscience (Poeppel and Embick 2005). For the specific problem of nested non-adjacent dependency acquisition, the connecting link between the fields was found across the ‘operations’ of each domain by associative, statistical learning and plasticity (Fig. 4.1, yellow/blue arrow at the bottom). The application of this type of learning was motivated be the observation that it played a central role in both fields. While the acquisition of non-adjacent grammars during passive listening was hypothesised to be supported by unsupervised associative learning (Mueller et al. 2018a), STDP was identified as a central associative learning mechanism in the brain (Dan and Poo 2006; Markram et al. 2011). Importantly, the application of STDP in a recurrent neural network model made it possible to also draw an explanatory link across the ‘elements’ of linguistics and neuroscience (Fig. 4.1, yellow/blue arrow on top). Here, the emerged synapse assemblies were a natural way for encoding the stimulus elements and transitions of nested non-adjacent dependencies. This encoding included that synapse assemblies reflected the accumulated stimulus statistics by their strengths, a hypothesised way of neural networks to encode environmental statistics in general (Bogaerts et al. 2022). Taken together, the ‘interface problem’ framework for linguistics and neuroscience (Poeppel and Embick 2005) provided a very useful scaffold for bridging the gap between these fields. As the ‘interface problem’ is present across all cognitive domains (Pulvermüller et al. 2014), the approach to focus on potential connections between ‘operations’, ‘computations’ (Carandini 2012) or ‘algorithms’ (Love 2015; Griffiths et al. 2015) and ‘elements’ of the domains of interest might be essential for the identification of even more ‘brain-cognition’ interfaces.

4.1.2 Implications for linguistics

Next to establishing an explanatory link between linguistics and neuroscience, the findings of this thesis further have important implications for reconsidering within-

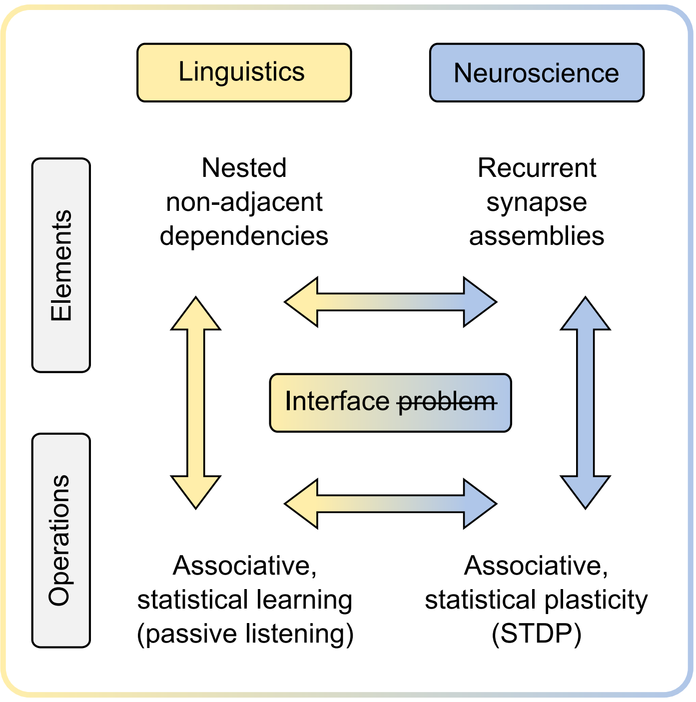


Figure 4.1: Overcoming the 'interface problem' between linguistics and neuroscience for nested non-adjacent dependency acquisition. Arrows indicate explanatory relations of elements and operations within (vertical) and across (horizontal) disciplines. Compare Fig. 7.1. in Poeppel and Embick (2005).

field links between 'operations' and 'elements'. In this thesis, the acquisition of nested NADs was successfully modelled by associative statistical learning with a training procedure where grammars were merely presented to the model, thereby mimicking the passive listening paradigm. In linguistics, the role of statistical, associative learning for grammar and language acquisition (Fig. 4.1, yellow vertical arrow) is however controversially discussed. While statistical learning is widely considered a potential underlying mechanism for language acquisition (Perruchet and Pacton 2006; Romberg and Saffran 2010; Erickson and Thiessen 2015; Thiessen 2017; Saffran and Kirkham 2018; Mueller et al. 2018a), it is also criticised to be insufficient for explaining the mastering of language and its rich hierarchical structures (Chen et al. 2021; Rawski et al. 2021). Moreover, the role of associative, statistical learning is also challenged by the so called 'poverty of the stimulus' argument (Pullum and Scholz 2002; Berwick et al. 2011) and the 'universal grammar' hypothesis (Yang 2004; Lidz and Gagliardi 2015; Friederici et al. 2017). Both lines of thought assume that the raw speech signal does not contain the necessary information for learning language from scratch. Rather, 'innate language knowledge' is seen as a guiding framework during the acquisition process (Lidz and Gagliardi 2015; Shi et al. 2020). However, more differentiated views consider 'universal grammar' as one essential factor next to others, like language experience and domain-general learning mechanisms (Yang et al. 2017). In support of critical views on the 'poverty of the stimulus' argument and the 'universal grammar' hypothesis (Lewis and Elman 2002; Perfors et al. 2006; Dąbrowska 2015; Chater and Christiansen 2018), this thesis contributed towards elucidating further the potential scope of associative, statistical learning. Here, the finding that a purely associative learning mechanism successfully modelled human grammar learning performances under various stimulus conditions was taken as a strong argument for considering it as a central contributor to language acquisition (Lehfeldt et al. n.d.). Moreover, a generic and randomly connected network, i.e. a purely naive architecture, was the substrate of NAD learning. Further, the network only had access to the grammars during sequential presentation and subsequent online processing, so that learning was purely stimulus-driven. Successful NAD learning in such a linguistically unbiased network architecture and with a training procedure resembling the passive-listening paradigm further strengthened the assumption that associative, statistical learning might be an important mechanism especially for early language acquisition phases. Taken together, the major role of associative, statistical learning for language acquisition might be characterised as allowing for the acquisition of statistically relevant structures of the perceived language input and thereby, also allowing for the formation of early knowledge representations.

4.1.3 Implications for neuroscience

The results of this thesis were conform with the idea of assembly-based cognition in neuroscience (Pulvermüller et al. 2014; Papadimitriou et al. 2020; Kossio et al. 2021), i.e. that STDP leads to the emergence of distributed stimulus representations in form of synapse assemblies (Fig. 4.1, blue vertical arrow). Further, this thesis demonstrated that STDP is not only a brain mechanism of basic memory formation problems (Dan and Poo 2006), but was also applicable to higher-order cognitive tasks like human grammar acquisition. This further strengthens STDP as a central learning mechanism of the brain and expands the model's scope of applicability from explaining low-level brain dynamics to high-level cognition. Moreover, a central challenge in the field of neuroscience is to understand how different time scales of neural encoding, learning and behaviour ranging from milliseconds, seconds to minutes and hours combine (Melamed et al. 2004; Drew and Abbott 2006; Setareh et al. 2018; Gerstner et al. 2018; Brzosko et al. 2019; Cone and Shouval 2021). Here, the implemented spiking RNN demonstrated that currently active stimuli can be represented by the instantaneous spiking activity of neurons. Learning, however, took place on slower time scales by the continuously evolving synaptic weights that were updated according to the processed spiking activity. Thus, considering the (spiking) brain as a hybrid system with both very fast and slow variables interacting with each other (Stimberg et al. 2014) might explain how arbitrary time scales are complemented via different brain variables (Kiebel et al. 2008; Castellano and Pipa 2013). In this thesis, temporal STDP windows for the induction of potentiation and depression were further examples for such an interaction on different time scales. While the temporal windows were defined by the decay of phenomenological memory traces taking place on comparably slow time scales, instantaneous spikes occurring within theses windows triggered plasticity changes. The time constants applied in this thesis (i.e. $\tau_P = 700$ ms and $\tau_D = 100$ ms), however, exceeded the electrophysiologically measured time windows in rats (Markram et al. 1997; Bi and

Poo 1998; Debanne et al. 1998; Bi and Poo 1999; Feldman 2000; Sjöström et al. 2001; Froemke and Dan 2002) which are usually applied accordingly in STDP models (Miner and Triesch 2016; Klos et al. 2018). Though this might be viewed as a critical deviation from the biological evidence, the rationale behind this extension of time constants was to explore if the core STDP algorithm was applicable to learning problems taking place on larger time scales (Testa-Silva et al. 2010). As the evidence of temporal STDP windows in humans is scarce (Koch et al. 2013), testing parameter spaces 'fitted' to the time scales of higher-level cognitive learning tasks currently remains a practicable solution for this endeavour. Next to the interaction of slow and fast brain variables, also memory itself is expressed at different time scales ranging from short- to long-term memory (Zucker and Regehr 2002; Tetzlaff et al. 2012; Benna and Fusi 2016). In this thesis, time scales of memory were expressed by an activity dependent weight decay, i.e. a short- to long-term memory transition (SLMT) mechanism (Lehfeldt et al. n.d.). Here, memory on different time scales was modelled in a conceptual fashion, implementing its transition according to the STDP learning protocol equivalently acting on a plastic weight decay. On the one hand, SLMT served as a practicable solution in order to prevent unstable runaway dynamics during grammar learning experiments. However, a further motivation was to include the concept of forgetting into the learning model (Richards and Frankland 2017). Studies implementing different forms of (adaptive) weight decay already acknowledged forgetting as a beneficial property of learning models (Panda and Roy 2017; Panda et al. 2018; Harrison et al. 2020; Endress and Johnson 2021). Throughout, a main contribution of forgetting was interpreted as de-noising the formed memory (Panda et al. 2018), i.e. as reducing the impact of outdated information (Hintzman and Ludlam 1980; Servan-Schreiber and Anderson 1990; Hintzman 1984; Yalnizyan-Carson and Richards 2022). Taken together, the ability of STDP to detect invariant structure in the input (Sprekeler et al. 2007) apparently can further be supported by memory decay or forgetting. Also in this thesis, this beneficial effect was observed as learning with SLMT led to strong and persistent grammar encodings while non-grammar encodings were comparably weaker and less persistent.

4.1.4 Revisiting the 'low-high' and 'subsymbolic-symbolic' debates

The finding that a low-level brain mechanism of associative, statistical learning implemented in a distributed neural network was successful in forming meaningful grammar representations made revisiting the 'low-high' and 'subsymbolic-symbolic' debates very intriguing. When integrating the results of this thesis into the previously identified 'low-high' and 'subsymbolic-symbolic' scales (Fig. 1.1), a shift of high-level human NAD learning performances from the symbolic into the subsymbolic domain became possible (Fig. 4.2). This was motivated by the fact that low-level and subsymbolic grammar representations, expressed via recurrent synapse assembly weight distributions, already matched human NAD learning performances. Apparently, the low-level and subsymbolic STDP mechanism was sufficient to achieve a cognitively meaningful encoding of NADs. This, in turn, further

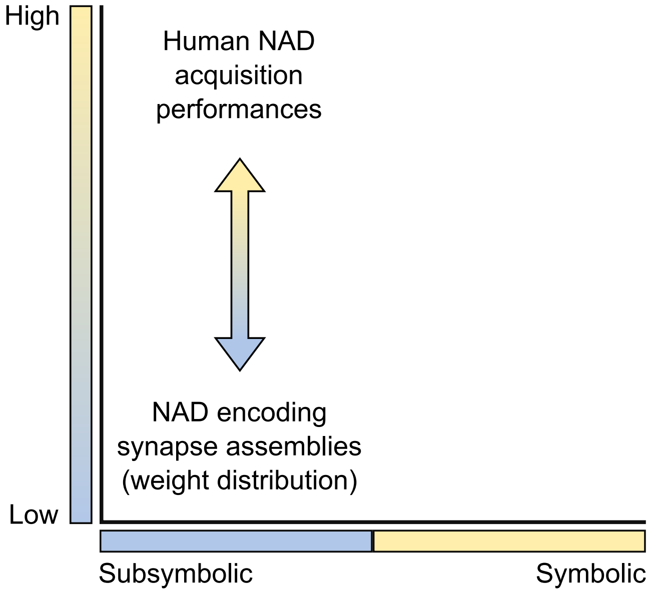
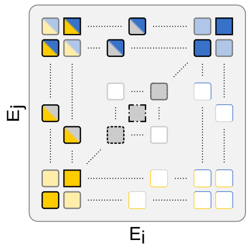
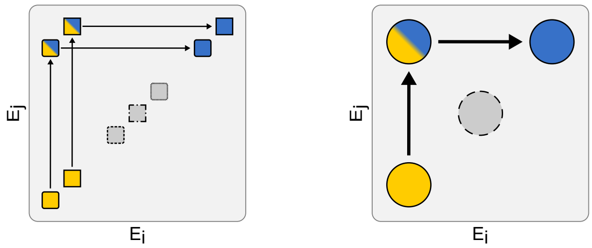


Figure 4.2: Integration of grammar learning experiment results into 'low-high' and 'subsymbolic-symbolic' scales. Low-level and subsymbolic NAD encoding synapse assemblies (i.e. their weight distribution) complied with high-level human NAD acquisition performances. This motivated a potential shift to the subsymbolic/high domain.

led to the possibility that higher-order grammar learning performances are not necessarily fully based on purely symbolic encodings and operations. Even though the nature of additional operation mechanisms impacting the human learning outcome remains elusive, the modelling results of this thesis are at least an indicator that such high-level cognitive skills might as well be performed in the subsymbolic domain. Further, subsymbolic knowledge representations acquired via spike-based statistical learning in the recurrent synapses might represent a potential basis for further linguistic operations (Fig. 4.3(a)). This thesis can be considered as modelling an early stage during language learning that primarily was concerned with the acquisition of distributional statistical knowledge. However, later phases of the language acquisition process possibly also include an evaluation of the structural and temporal composition of grammars, i.e. an analysis of the nesting levels. This might require that, a priori, correct pair associations between grammatical A and B elements have been learned. Further, a nesting level analysis probably also relies on knowledge about the correct temporal within-pair order, i.e. that a B element will follow after experiencing its grammatical A element. In this regard, the grammatical A to B transition assemblies (i.e. $\lambda : A \rightarrow B$) encoded both the correct pair associations of grammatical A and B elements as well as their temporal within-pair orders (Fig. 4.3(b)). A further linguistic operation might deal with the extraction of the general tendency of experienced stimuli, i.e. a generalisation of rules. This might require that, a priori, a sufficiently high number of individual grammar samples following a



(a) NAD encoding synapse assemblies



(b) Template for nesting level analysis?

(c) Template for generalisation?

Figure 4.3: NAD encoding synapse assemblies as templates for further linguistic operations? (a) NAD encoding synapse assemblies: strengths encode the accumulated statistics of all stimulus elements and transitions. (b) Potential template for nesting level analysis: $\lambda : A \to B$ encode correct associations and temporal within-pair orders. (c) Potential template for generalisation: extraction of general tendency from all individual NAD samples.

shared rule has been experienced and learned. Further, some abstraction or summation mechanism, or probably a higher-order brain region, could subsequently extract the general tendency of the individually learned examples and derive a generalised representation (Fig. 4.3(c)). Here, the recurrent synapse assemblies encoded the strengths of all individual element pairs and transitions, such that A to B transition assemblies (i.e. $\lambda : A \to B$) might be detected as a strong and generally persistent structure. Thus, the learned synapse representations might be viewed as an informative template that a potential generalisation mechanism could rely upon. That low-level knowledge representations might support subsequent analysis steps of higher-order cognitive skills is conform with the idea of an 'integrated' view on cognition where subsymbolic representations underlie symbolic ones (Kelley 2003). However, understanding how symbolic cognitive computations arise from neural operations is still an ongoing process (Smolensky 2012; Alhama and Zuidema 2019; Mastrogiuseppe et al. 2022). Still, the findings of this thesis support the notion that higher-level brain regions might compute over low-level sensory representations (Näätänen et al. 2001) and further, that (statistical) language acquisition might rely on the extraction of distributed cues and subsequent, potentially more symbolic-like, integration processes (Endress and Bonatti 2007; Thiessen et al. 2013; Erickson and Thiessen 2015).

4.2 Possible future directions

4.2.1 Including the 'perception-cognition' interface

Cognition is tightly interlinked with the representations formed at the sensory periphery and therefore with perception (Mesulam 1998; Näätänen and Winkler 1999; Munkong and Juang 2008; Wolff et al. 2021). The importance of low-level brain mechanisms becomes especially apparent in auditory cortex, where 'primitive' forms of cognition are hypothesised to exist as reflected by pre-attentive forms of sensory input transformations (Näätänen et al. 2001). Further, language acquisition performance relies on auditory sensory processes (Mueller et al. 2012). Moreover, with regard to grammar learning, the stimulus properties of the speech signal itself have been shown to influence the learnability (Nespor et al. 2003; Bonatti et al. 2005; Toro et al. 2008a; Toro et al. 2008b; Fogerty and Humes 2012), though see Weyers and Mueller (2022). However, as the link between perceptual and cognitive processes is not fully understood, the importance to include sensory encoding schemes in the design of cognitive (language learning) models becomes highlighted. In this context, the distributed encoding scheme of the RNN model of this thesis opens the possibility to approach this problem further by studying language learning based on auditory spike representations (Fontaine et al. 2011). To illustrate, spiking training sequences implemented grammar feature variations ranging from the temporal structure, occurrence frequency to stimulus strengths in a low-level and distributed manner. However, in order to understand the 'perception-cognition' interface better, ecologically more informative stimuli could be used. In particular, the applied Poisson spike patterns can be viewed as ecologically 'meaningless' as they primarily encoded the strength of a stimulus reflected by the firing rate. In contrast to these Poisson spike trains, spatio-temporal spike representations derived from sound or speech signals might be more informative stimuli (Holmberg and Hemmert 2004; Holmberg et al. 2005; Liu et al. 2010; Klampfl and Maass 2013; Yu et al. 2019). These are also referred to as 'spikegrams' (Zai et al. 2015) and have the great potential to extend training stimuli by essential sound or speech signal properties, as for example temporal information (Purwins et al. 2000; Rankin and Rinzel 2019). In summary, cognitive models that include subsymbolic and distributed encoding schemes are candidates to implement details about sensory stimulus representations in their inputs. Thus, they have the potential to advance understanding the formation of meaningful percepts and to elucidate further the influence of low-level brain mechanisms on higher-order cognitive skills.

4.2.2 Precursor linguistic abilities across species?

Despite the uniqueness of the human language faculty (Berwick et al. 2013), the discovery of shared processing or learning principles across humans and animal species is a promising approach for identifying low-level brain mechanisms that possibly support high-level cognitive skills such as language (van Horik and Emery 2011; Steinschneider et al. 2013; Lattenkamp and Vernes 2018; Levelt 2018; Corballis 2020; Suzuki 2021). A bandwidth of potential evidence about precursor linguistic abilities in non-human animals exists. For example, rodents showed an ability to discriminate syllables based on voicing contrast (Kuhl and Miller 1975). Further, rats could discriminate languages (Toro et al. 2003), segment speech (Toro and Trobalón 2005), generalise acoustic patterns (Toro and Hoeschele 2017) and learn acoustic rules (de la Mora and Toro 2013). Moreover, in birds, visual artificial grammar learning (Stobbe et al. 2012) and auditory syntactic rule discrimination (Abe and Watanabe 2011) has been shown. In primates, finite state grammar learning (Fitch and Hauser 2004), adjacent dependency learning (Englund et al. 2022), but also NAD processing (Watson et al. 2020), associative learning of center embedded grammars (Rey et al. 2012) and the production of embedded movement sequences (Jiang et al. 2018) has been demonstrated. However, potential evidence about preliminary forms of linguistic proficiency in non-human animals is hotly debated (Beckers et al. 2012; Poletiek et al. 2016; Rawski et al. 2021; Watson et al. 2021). Mostly, the design of comparative language acquisition studies is considered inadequately for drawing far-reaching conclusions such as the existence of precursor linguistic abilities in animals. For example, the discrepancy between non-adjacent grammar stimuli and human syntax (Rawski et al. 2021) or between animal sequence production and human language production (Poletiek et al. 2016) is highlighted. Further, claims about precursor linguistic abilities are viewed as premature because reported learning abilities do not compare to the compositionality of human language (Beckers et al. 2012). Next to critically evaluating the findings of comparative experimental studies, computational modelling can contribute towards the identification of potentially shared processing principles (Yildiz et al. 2013) or organisational features of animal vocalisations and human language (Kershenbaum et al. 2014; Sainburg et al. 2019). Here, especially the general ability to process long-range dependencies is currently investigated as an important precursor ability for language (Sainburg et al. 2022). Moreover, the performance of possibly underlying learning mechanisms can be studied, such as done in this thesis by testing domain-general, associative learning. Notably, the STDP learning model was originally derived based on electrophysiological evidence in rats (Markram et al. 1997; Bi and Poo 1998; Debanne et al. 1998; Bi and Poo 1999; Feldman 2000; Sjöström et al. 2001; Froemke and Dan 2002). Despite being a non-human learning algorithm, its success in modelling a variety of human-specific grammar acquisition patterns was interpreted as an indicator that STDP might not only represent an important low-level prerequisite for language but is presumably also shared across species (Lehfeldt et al. n.d.). Further, the applicability of STDP for modelling the acquisition of human grammatical structure on a low-level conforms with the idea that language acquisition might rely on both evolutionary 'old' and more recent cognitive strategies (Toro 2016). Especially the proficiency in serial analysis is viewed as one important skill for language, next to segmentation, categorisation and abstraction (Kiggins et al. 2012), whereby STDP might be a potential candidate for such sequence processing and learning abilities. Taken together, the results of this thesis showed that neural modelling studies can contribute new insights into the linguistic capacities of low-level (and non-human) brain mechanisms. The insights gained here might be worthy of discussion in comparative lines of research dedicated to the evolutionary origins of language (Hauser et al. 2002; Sherwood et al. 2008; ten Cate and Okanoya 2012; Kiggins et al. 2012; Bowling and Fitch 2015; Wilson et al. 2018; Mueller et al. 2018b).

4.2.3 A possible template for neuromorphic applications

Software models of spiking neural networks serve as valuable templates for developing hardware implementations of brain circuits and function (Zenke et al. 2021; Guo et al. 2021), i.e. so called neuromorphic models (Mead 1990; Douglas et al. 1995b). The aim to develop computing devices that make use of the information processing and learning principles of biological brains has gained increasing attention over the last years (Indiveri and Horiuchi 2011; Poon and Zhou 2011; Monroe 2014; Hamilton et al. 2014; Furber 2016; Knight et al. 2016; Thakur et al. 2018; Neftci 2018; Strukov et al. 2019; Roy et al. 2019; Kendall and Kumar 2020; Zhang et al. 2020b; Ielmini et al. 2021; Kim et al. 2021; Bartolozzi et al. 2022; Mehonic and Kenyon 2022; Venkatesan and Williams 2022). So far, the field of neuromorphic engineering has brought fourth a variety of spike-based hardware applications based on principles of sensory processing ranging from the visual (Mead and Mahowald 1988; Chen et al. 2020; Gallego et al. 2022), auditory (Liu et al. 2010; Jiménez-Fernández et al. 2017), olfactory (Jürgensen et al. 2021) to the tactile domain (Rongala et al. 2017; Osborn et al. 2018; Sengupta et al. 2022). But also spike-based learning systems have been developed giving rise to the possibility of implementing cognitive skills in neuromorphic hardware (Indiveri et al. 2009; Neftci et al. 2013; Indiveri and Douglas 2014; Chicca et al. 2014). Here, for example, learning applications range from pattern classification (Mitra et al. 2009; Schmuker et al. 2014; Patiño-Saucedo et al. 2020; Kugele et al. 2020), pattern learning and recall (Milo et al. 2018), pattern learning and retrieval (Fang et al. 2022) to prediction (Debat et al. 2021) and decision making (Corradi et al. 2015; Liang and Indiveri 2019; Pedretti et al. 2020). As neuromorphic systems rely on event-based neural and synaptic dynamics, exploring the possibility to apply the developed training stimuli and implemented learning model of this thesis in such hardware applications might be a promising approach for extending state-of-the-art neuromorophic systems by grammar learning performances. Taken together, studying cognitive computation in spike-based models not only contributes towards a better understanding of its low-level implementation in the neural substrate. It also contributes towards the potential transfer of modelled cognitive skills into computing devices that are based on brain principles.

4.3 Conclusion

4.3.1 Diverse strategies for navigating a diverse world

A large variety of theories about how the brain ‘makes sense’ of the world, learns its principles and rules, adapts to its constraints or foresees future scenarios has been developed in the field of cognitive neuroscience. While this thesis laid a special focus on associative, statistical learning and its potential low-level implementation in the neural substrate of the brain, it is clear that a huge bandwidth of complementary learning principles and strategies exists in order to understand and, ultimately, to navigate the world. Thus, beyond ‘associative’ (Hebb 1949), ‘unsupervised’ (Barlow 1989) or ‘statistical’ (Thiessen 2020; Sherman et al. 2020) learning, additional classes of learning range from ‘reinforcement learning’ (Kaelbling et al. 1996; Dayan and Niv

2008; Niv 2009; Arulkumaran et al. 2017; Neftci and Averbeck 2019), 'supervised learning' (Knudsen 1994; Raymond and Medina 2018), to 'predictive coding' (Bubic et al. 2010; de-Wit et al. 2010; Huang and Rao 2011; Clark 2013; Hull 2020) and 'free energy' principles (Friston 2005; Friston 2009; Friston 2010; Friston et al. 2018). Further, action-based learning and exploration strategies are described by theories of 'embodied cognition' (Anderson 2003; Adams 2010; Engel et al. 2013; Foglia and Wilson 2013; Wilson and Golonka 2013; Badcock et al. 2019) and 'curiosity-driven cognition' (Gottlieb et al. 2013; Oudeyer and Smith 2016; Gottlieb and Oudeyer 2018; Schwartenbeck et al. 2019; Ten et al. 2021). This (certainly still incomplete) collection of learning classes highlights the rich repertoire of cognitive mechanisms and strategies that the brain (and active agents) can rely upon when faced with a task or problem to solve. However, theses mechanisms potentially do not work in perfect isolation but rather interact in dynamic ways. Therefore, a major challenge for future research is to understand how these different learning mechanisms and strategies work together (Orpella et al. 2021; Lang et al. 2022) in order to give rise to intelligent behaviour and cognition. Taking unsupervised, reinforcement and supervised learning schemes as an example, they are hypothesised to be predominant mechanism of cortex, basal ganglia and cerebellum, respectively (Doya 1999; Doya 2000). However, to which degree these isolated learning types interact and support each other is still subject of recent investigations (Caligiore et al. 2019; Badakva et al. 2020). Moreover, it remains to be shown if they are activated in a demand-driven way, i.e. corresponding to the encountered learning scenario that either provides no feedback, reinforcing signals or teacher cues that might be exploited. But finally, also understanding better to which extent (cognitive) behaviours are pre-defined genetically (Zador 2019) or by evolutionary processes (Hasson et al. 2020) will contribute towards a holistic picture of the underlying mechanisms of cognition. Taken together, a full understanding of cognition certainly requires an integration across a variety of scales, from low- to high levels of analysis, subsymbolic to symbolic encoding or processing schemes but also comparatively across species. Moreover, by considering the diversity of tasks encountered in the world, a diverse set of cognitive mechanisms needs to be understood in relation to each other (Wörgötter and Porr 2005). By demonstrating the importance of low-level brain mechanisms for high-level cognitive skills, the present thesis contributed to this endeavour and furthermore, provided a missing piece to the great 'brain-cognition' interface puzzle. To which extent this contribution gives rise to the discovery of more connecting links between brain and cognition remains to be explored in the future.

Appendix A

Complete collection of separability measures: figures

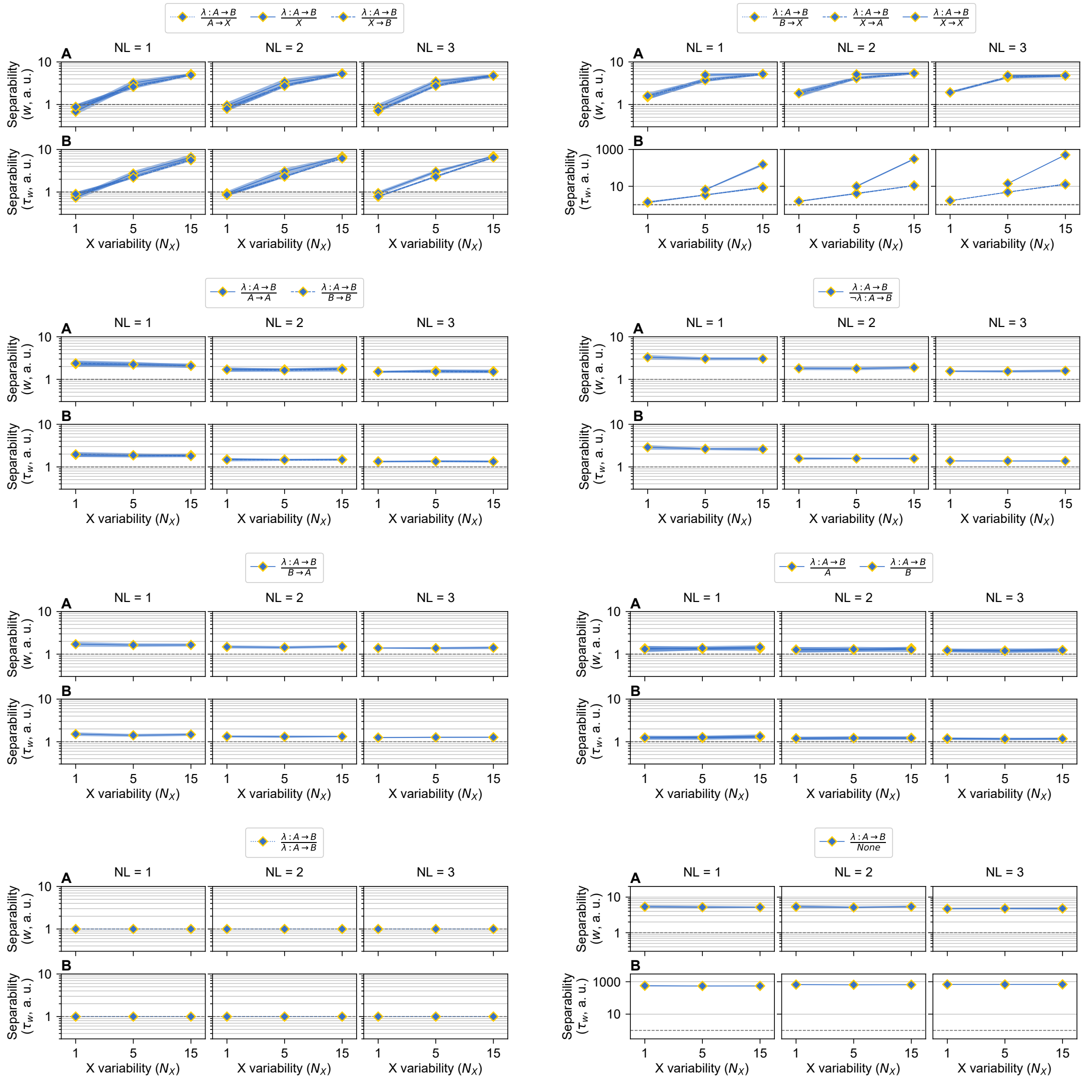


Figure A.1: Separability measures of w and τ_w in the experiment 'X variability' (reference $\lambda : A \to B$).

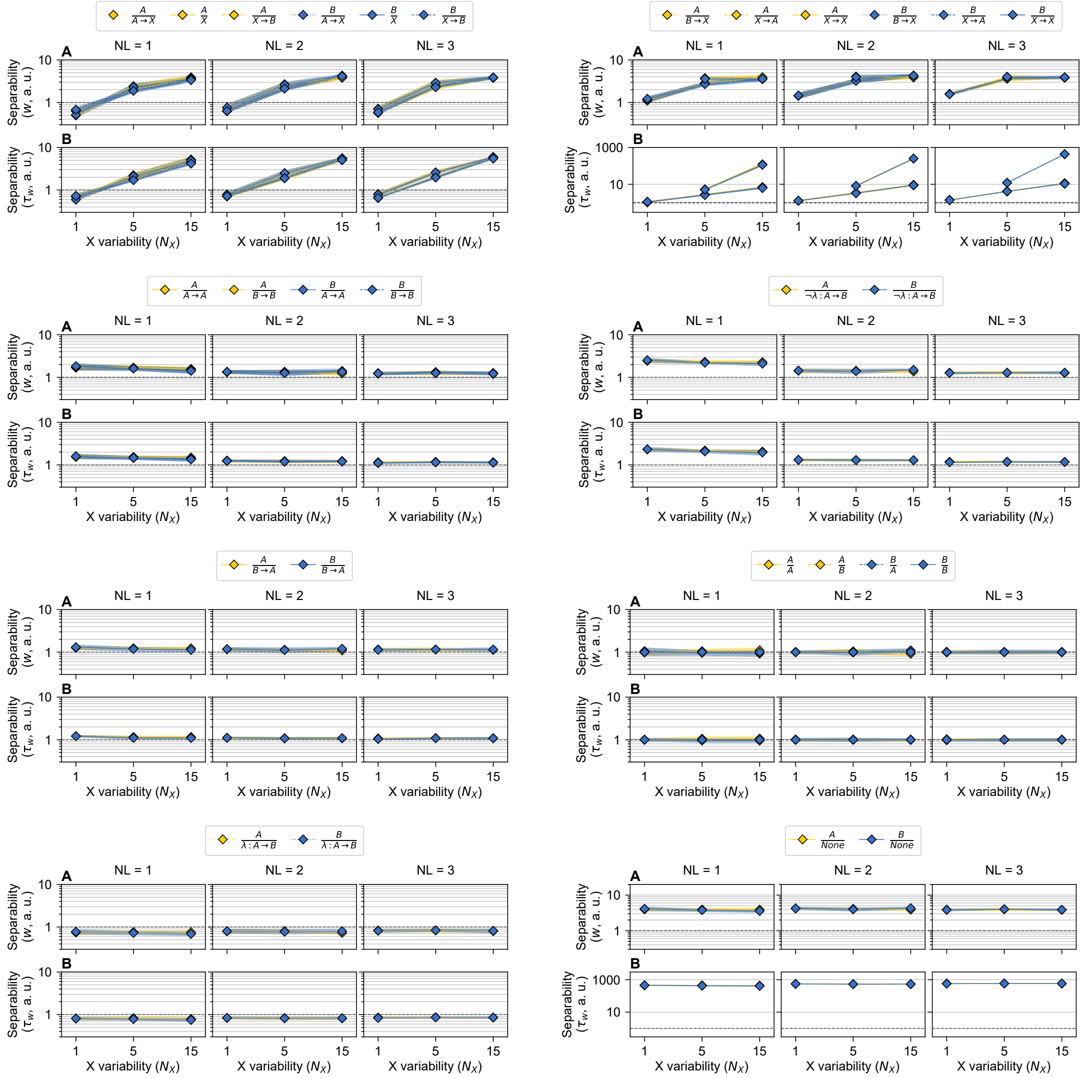


Figure A.2: Separability measures of w and τ_w in the experiment 'X variability' (references A and B).

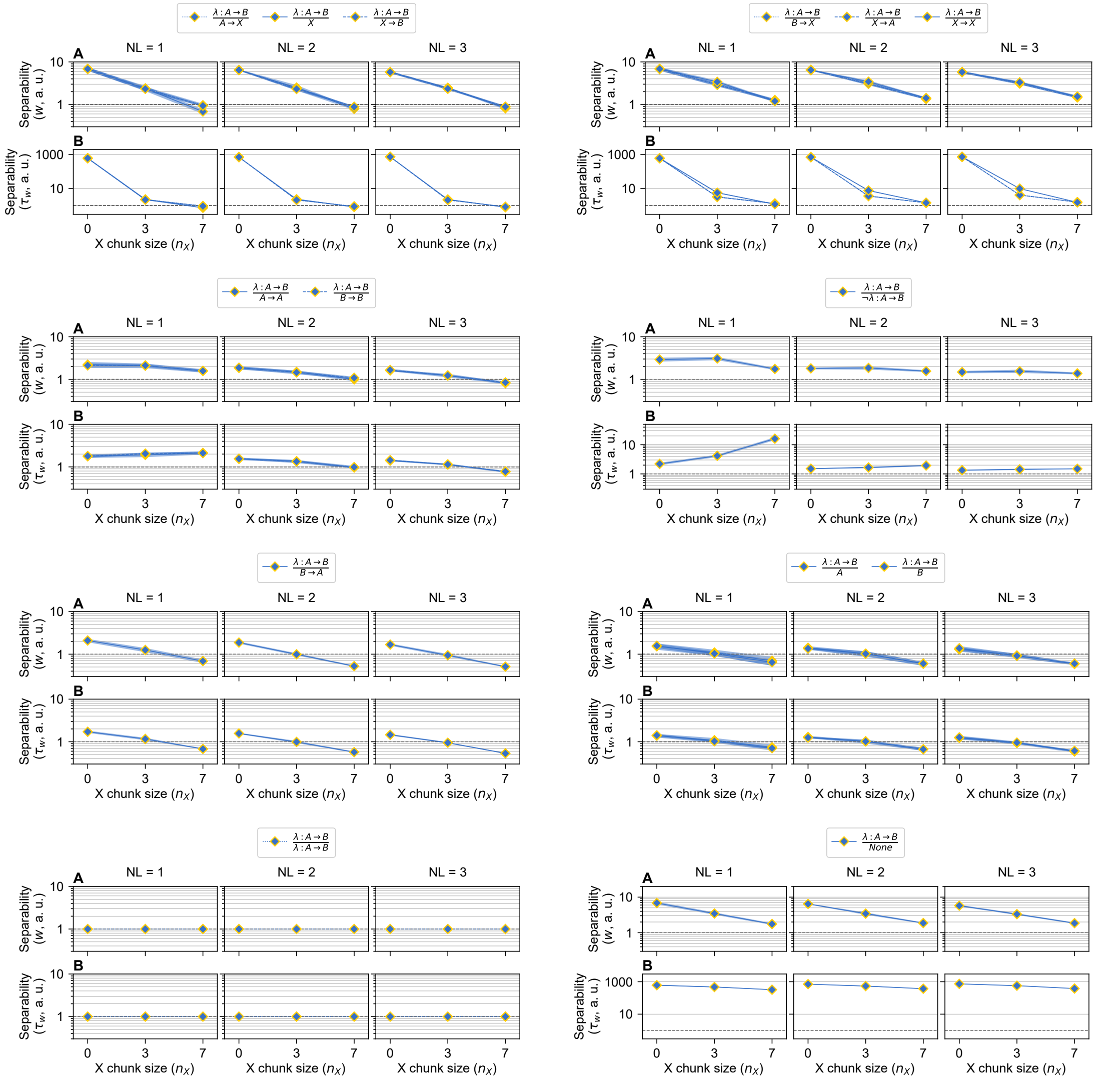


Figure A.3: Separability measures of w and τ_w in the experiment 'X chunk size' (reference $\lambda : A \to B$).

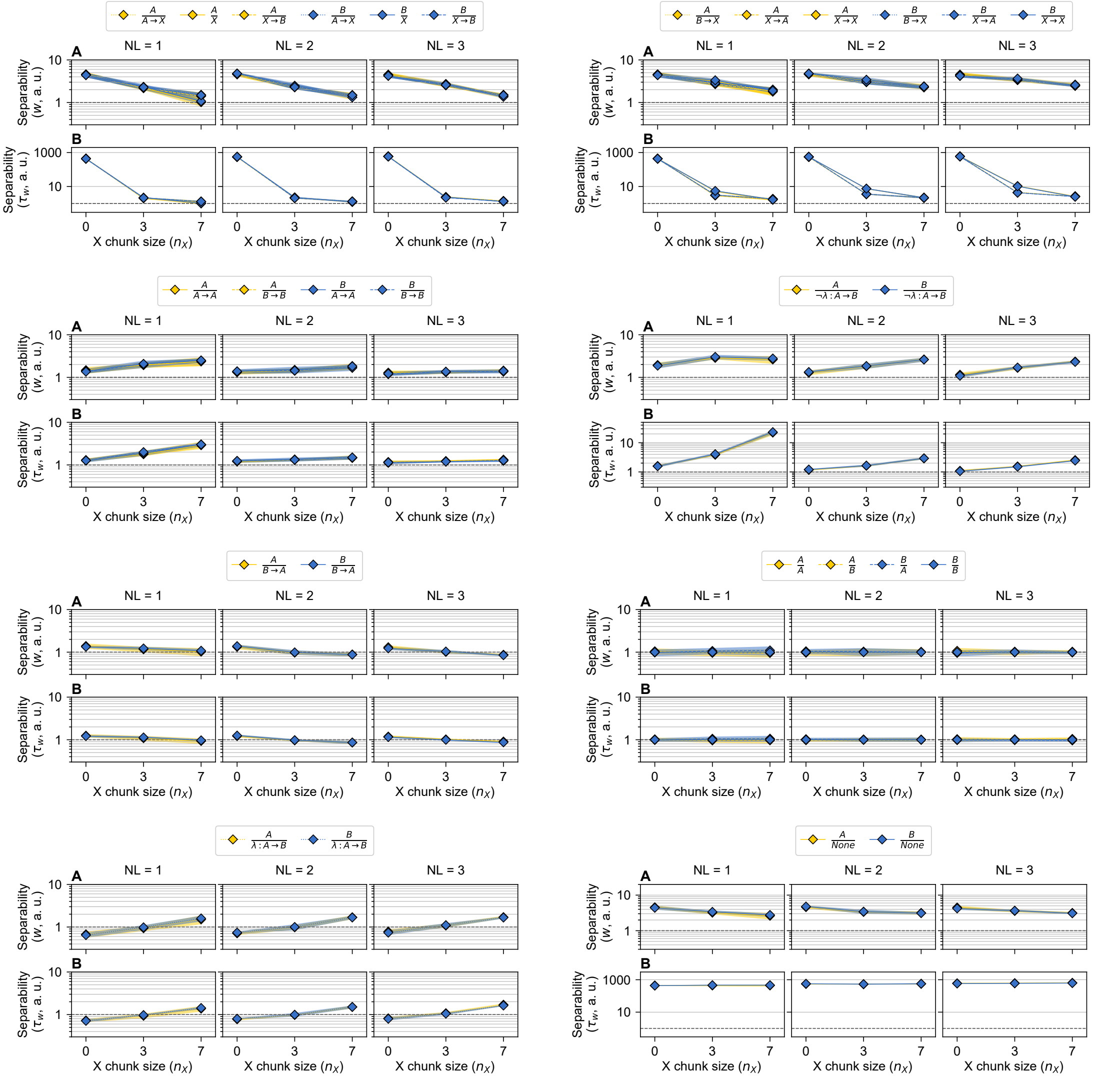


Figure A.4: Separability measures of w and τ_w in the experiment 'X chunk size' (references A and B).

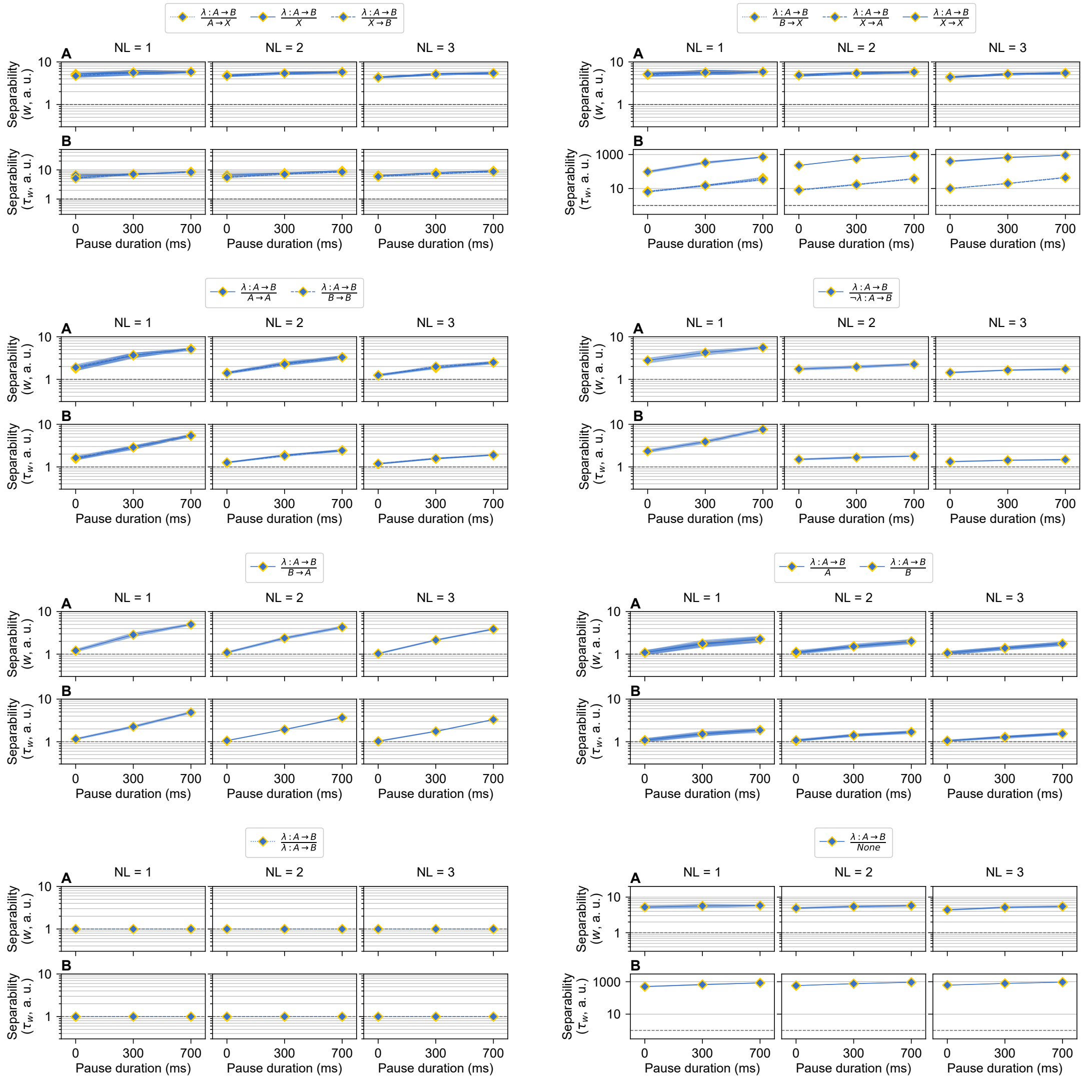


Figure A.5: Separability measures of w and τ_w in the experiment 'Pause variability' (reference $\lambda : A \to B$).

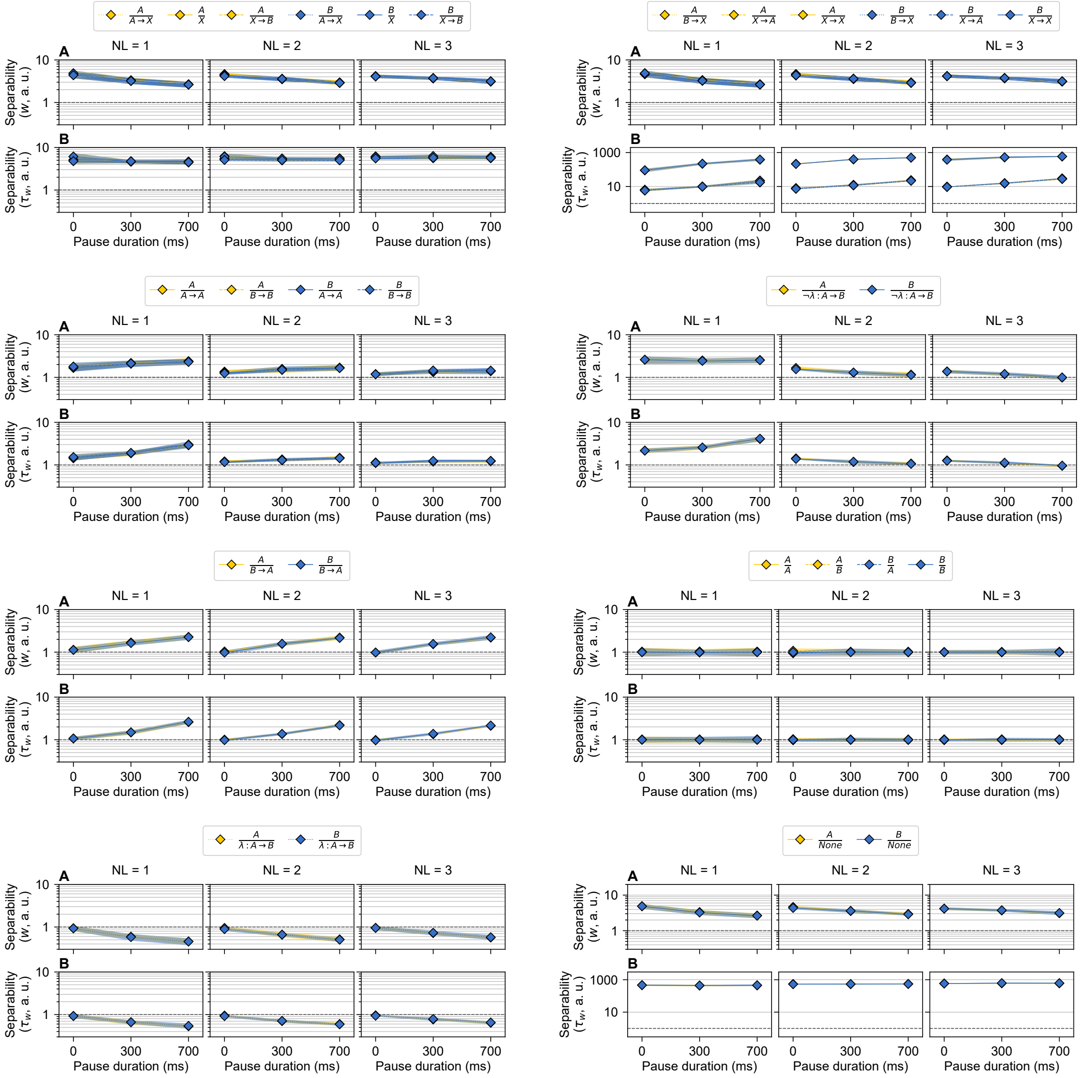


Figure A.6: Separability measures of w and τ_w in the experiment 'Pause variability' (references A and B).

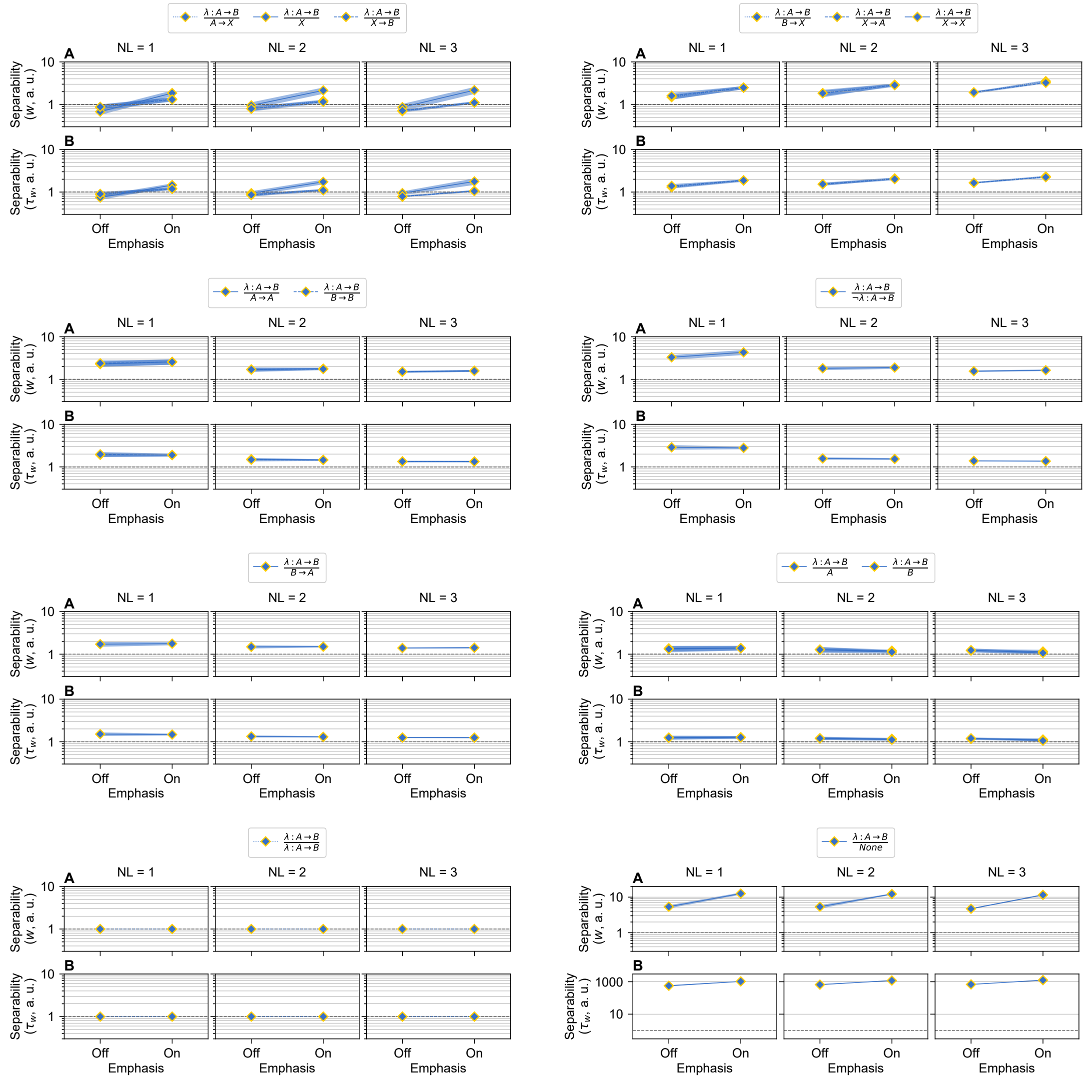


Figure A.7: Separability measures of w and τ_w in the experiment ‘Emphasis’ (reference $\lambda : A \to B$).

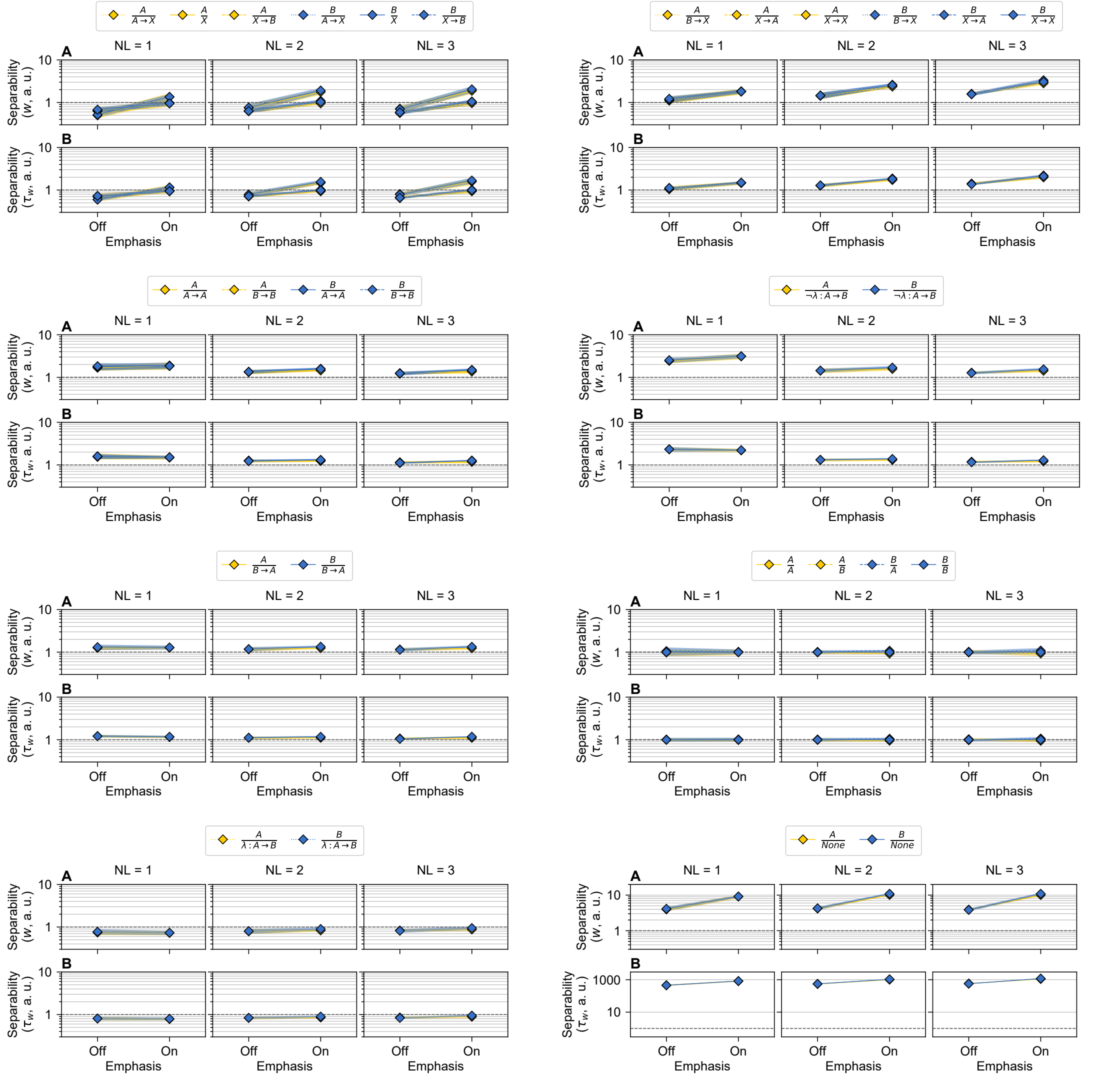


Figure A.8: Separability measures of w and τ_w in the experiment ‘Emphasis’ (references A and B).

List of Figures

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