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DOCTORAL THESIS

THE INTERPLAY OF SIMULATION MODELS AND NEUROIMAGING: ASSOCIATIVE AND SEMANTIC EFFECTS ON LEXICAL PROCESSING

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DECLARATION OF AUTHORSHIP

I, Andre Rölke-Wellmann (born on January 25th 1986 in Frankfurt am Main), confirm that this doctoral thesis titled "**THE INTERPLAY OF SIMULATION MODELS AND NEUROIMAGING: ASSOCIATIVE AND SEMANTIC EFFECTS ON LEXICAL PROCESSING**" as well as the included publications (STUDY A, STUDY B, STUDY C) are of my own work.

Frankfurt am Main, 20.05.2021

Place and Date Signature

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ABSTRACT

The visual processing of a word is influenced by lexical properties, such as the number of letters, word frequency and predictability, and also by the relationship to preceding and succeeding words. The manipulation of these variables affects the response time, error rate, fixation duration and brain activity elicited by that word.

Recent research suggested that text corpus data can be used to calculate the direct association of two words by counting their statistical co-occurrence in a sentence. The semantic similarity can be captured by the number of common direct associations. In theory, this should allow a clear separation of direct association from semantics, which was previously reported not to be possible when relying on subjective methods like free association norms. Hence, the first major research objective of the present doctoral thesis was to provide evidence for the dissociation of the two relationships. In STUDY A, a primed lexical decision task was conducted, while the prime-target relation was manipulated by their direct association (strong/no) and the number of common associates (many/no). Response time data revealed that both types contributed to the target priming additively, thus independently from each other. Moreover, priming by direct association increased at a long stimulus onset asynchrony (SOA), whereas many common associations primed the target at the short SOA, only. This pattern is consistent with classic findings in the literature, confirming the proposal that word co-occurrences can produce both priming effects.

Word co-occurrences have been implemented into a multilayer model, the Associative Read-Out Model (AROM), to predict associative effects during visual word recognition (e.g. Hofmann & Jacobs, 2014). Hofmann and Jacobs (2014) proposed that the semantic layer of the AROM corresponds to the function of the left inferior frontal gyrus (LIFG) to regulate semantic conflicts. STUDY B examined the functional connectivity of the LIFG during semantic priming, since the control of semantic influences by the prime is essential for the correct identification of the target. Functional magnetic resonance imaging data showed that the LIFG interacted with the fusiform gyrus, the hippocampus, the anterior cingulate cortex and the orbitofrontal cortex to resolve semantic mismatches. As the orthographic level of the AROM reflects the function of the fusiform gyrus, the assumed connection between the semantic and the orthographic layer could be confirmed. The results further imply that the hippocampal system plays a critical role during semantic processing. Therefore, the AROM was extended by a conjunctive layer (c-AROM) in the present thesis to illustrate the hippocampal mechanism of pattern separation. It was assumed that distinct features of a word contribute to better memory encoding and retrieval. First simulation data demonstrate that the model can now predict recognition memory in a biologically plausible way.

During natural reading, there are diverging theories whether words can be processed in serial or in parallel. A serial processing would imply that top-down lexical information from a word in the parafovea cannot affect the currently fixated word. STUDY C utilized the first fixation on a word as marker for the corresponding hemodynamic response, which was recorded by functional near-infrared spectroscopy (fNIRS). A target word in every sentence was manipulated by its frequency (high/low) and predictability (high/low). At the fixation of the pre-target word, neural activation in the left occipital cortex increased if the following target word was infrequent and unpredictable. This indicates that higher order parafoveal information was accessible in parallel to the processing of the fixated word.

In summary, a novel co-occurrence based approach was used to elicit distinct priming patterns for direct associations and semantic relationships. It further allowed the prediction of ventral visual stream activation. For the first time in reported literature, eye movements were coregistered with fNIRS data to unravel the parallel processing of multiple words on a neurocognitive level. Based on these findings, models of visual word recognition and eye movement behavior can now improve in their biological plausibility. More applications and implications on the neuropsychological field are discussed.

ZUSAMMENFASSUNG

Die visuelle Wortverarbeitung wird durch lexikalische Eigenschaften wie Wortlänge, Worthäufigkeit, Vorhersagbarkeit, aber auch durch die assoziative Beziehung zu vorhergehenden oder nachfolgenden Wörtern beeinflusst. Eine Manipulation dieser Variablen schlägt sich wiederrum auf die Reaktionszeit, die Fehlerrate, die Fixationsdauer und die Gehirnaktivität zu diesem Wort nieder.

Neuste Forschungsergebnisse legen nahe, dass Textkorpusdaten verwendet werden können, um die direkte Assoziation zweier Wörter zu bestimmen, indem die Wahrscheinlichkeit ihres gemeinsamen Auftretens in einem Satz berechnet wird. Die semantische Ähnlichkeit kann durch die Anzahl der gemeinsamen direkten Assoziationen erfasst werden. Theoretisch sollte dieses komputationale Prinzip eine klare Trennung der direkten Assoziation von der Semantik ermöglichen. Dies galt zuvor als nicht möglich, wenn man sich auf subjektive Verfahren wie freie Assoziationsnormen berief. Das erste wichtige Forschungsziel der vorliegenden Doktorarbeit war daher, Belege für die Dissoziation der beiden Beziehungsgrade zu liefern. In STUDY A wurde eine lexikalische Entscheidungsaufgabe mit Priming durchgeführt, wobei die Prime-Zielwort Beziehung durch die direkte Assoziation (stark/keine) und die Anzahl der gemeinsamen Assoziationen (viele/keine) manipuliert wurde. Die Reaktionszeitdaten offenbarten, dass beide Beziehungsgrade additiv und somit unabhängig voneinander zum Priming des Zielwortes beitrugen. Darüber hinaus erhöhte sich das Priming durch die direkte Assoziation bei einer langen Dauer zwischen dem Einsetzen von Prime und Zielwort (SOA), während viele gemeinsame Assoziierte das Erkennen des Zielwortes nur bei der kurzen SOA erleichterten. Dieses Ergebnismuster deckt sich mit den typischen Befunden in der Literatur und bestätigt den Vorschlag, dass Wort-Kookkurrenzen beide Priming-Arten hervorrufen können.

Diese Wort-Kookkurrenzen wurden kürzlich in ein mehrschichtiges Modell implementiert, das Associative Read-Out Model (AROM), um assoziative Einflüsse während der visuellen Worterkennung vorherzusagen (z.B. Hofmann & Jacobs, 2014). Hofmann und Jacobs (2014) schlugen vor, dass die semantischen Ebene des AROMs v.a. der Funktion des linken inferioren Frontalgyrus (LIFG) entspricht, welcher semantische Konflikte reguliert. STUDY B untersuchte die funktionelle Konnektivität des LIFGs während des semantischen Primings, da hier die Regulation semantischer Einflüsse durch das Prime essentiell ist für die korrekte Identifikation des Zielwortes. Die Analyse von per funktioneller Magnetresonanztomographie gemessenen Bilddaten zeigte, dass der LIFG mit dem fusiformen Gyrus, dem Hippocampus, dem anterioren cingulären Cortex und dem orbitofrontalen Cortex interagierte um semantische Konflikte zu lösen. Da die orthografische Ebene des AROMs die Funktion des fusiformen Gyrus wiederspiegelt, konnte somit die angenommene Verbindung zwischen der semantischen und der orthografischen Ebene bestätigt werden. Die Ergebnisse deuten ferner darauf hin, dass das hippocampale System während der semantischen Verarbeitung eine entscheidende Rolle spielt. Daher

wurde das AROM in der vorliegenden Arbeit um eine konjunktive Ebene (c-AROM) erweitert, um den hippocampalen Mechanismus der Mustertrennung abzubilden. Hier wurde angenommen, dass distinkte Eigenschaften eines Wortes dazu beitragen, es besser lernen und wieder abrufen zu können. Erste Simulationsdaten zeigen, dass das Modell das Wiedererkennungsgedächtnis nun auf biologisch plausible Weise vorhersagen kann.

Bezüglich des natürlichen Lesens gibt es unterschiedliche Theorien, ob Wörter seriell oder parallel verarbeitet werden können. Eine serielle Verarbeitung würde bedeuten, dass lexikalische Top-Down-Informationen von einem Wort in der Parafovea das aktuell fixierte Wort nicht beeinflussen können. STUDY C verwendete die erste Fixation eines Wortes als Marker für die dazugehörige hämodynamische Antwort, die durch funktionelle Nahinfrarotspektroskopie (fNIRS) aufgezeichnet wurde. Pro Satz wurde ein Zielwort durch seine Häufigkeit (hoch/niedrig) und Vorhersagbarkeit (hoch/niedrig) manipuliert. Bei der Fixation des Präzielworts nahm die neuronale Aktivierung im linken Occipitalcortex zu, wenn das Zielwort selten und unvorhersehbar war. Dies deutet darauf hin, dass parafoveale Informationen höherer Ordnung parallel zur Verarbeitung des fixierten Wortes zugänglich waren.

Zusammenfassend wurde ein neuartiger Ansatz auf der Basis des gemeinsamen Auftretens zweier Wörter verwendet, um unterschiedliche Priming-Muster für direkte Assoziationen und semantische Beziehungen zu erfassen. Dies ermöglichte ferner die Vorhersage von Aktivierung entlang des ventralen visuellen Pfads. Zum ersten Mal wurden Blickbewegungen mit fNIRS-Daten koregistriert, um die parallele Verarbeitung mehrerer Wörter auf neurokognitiver Ebene aufzuzeigen. Basierend auf diesen Erkenntnissen können Modelle der visuellen Worterkennung und der Blickbewegung nun in ihrer biologischen Plausibilität optimiert werden. Weitere Anwendungen und Implikationen bezüglich des neuropsychologischen Gebiets werden diskutiert.

RESEARCH ARTICLES

STUDY A	Roelke, A., Franke, N., Biemann, C., Radach, R., Jacobs, A. M., & Hofmann, M. J. (2018). A novel co-occurrence-based approach to predict pure associative and semantic priming. *Psychonomic Bulletin & Review*, 25(4), 1488-1493.
STUDY B	Roelke, A., & Hofmann, M. J. (2020). Functional connectivity of the left inferior frontal gyrus during semantic priming. *Neuroscience Letters,* 735, 135236
STUDY C	Roelke, A., Vorstius, C., Radach, R., & Hofmann, M. J. (2020). Fixation-related NIRS indexes retinotopic occipital processing of parafoveal preview during natural reading. *NeuroImage*, 215, 116823.

CONTENTS

LIST OF ABBREVIATIONS

[deoxy-Hb]	Concentration of Deoxygenated Hemoglobin
[oxy-Hb]	Concentration of Oxygenated Hemoglobin
ACC	Anterior Cingulate Cortex
AIC	Akaike Information Criterion
AS	Associative Strength
AROM	Associative Read-Out Model
BOLD	Blood Oxygenation Level Dependent
DA	Direct Association
CA	Common Associates
CLS	Complementary Learning Systems
EEG	Electroencephalography
ER	Error Rate
FG	Fusiform Gyrus
fMRI	Functional Magnetic Resonance Imaging
fNIRS	Functional Near-Infrared Spectroscopy
FOV	Field of View
FWE	Family-Wise Error
FWHM	Full Width at Half Maximum
GLM	General Linear Model
HRF	Hemodynamic Response Function
IAM	Interactive Activation Model
LIFG	Left Inferior Frontal Gyrus
M	Mean Value
MNI	Montreal Neurological Institute
MTG	Middle (+Inferior) Temporal Gyrus
OC	Occipital Cortex
OFC	Orbitofrontal Cortex
PFC	Prefrontal Cortex
PG	Processing Gradient
PoF	Parafoveal-on-Foveal
PPI	Psychophysiological Interaction
ReML	Restricted Maximum Likelihood
RSVP	Rapid Serial Visual Presentation
RT	Response Time
SAS	Sequential Attention Shift
SD	Standard Deviation
TE	Time of Echo
TR	Time of Repetition
SOA	Stimulus Onset Asynchrony
VOI	Voxel of Interest
Wavelet-MDL	Wavelet Minimum Description Length Detrending

1 INTRODUCTION

1.1 WORD CORPORA AND THEIR APPLICATION IN INTERACTIVE ACTIVATION MODELS

Visual communication by symbols and words is one of the key achievements in human history. It allows to pass on information between generations with tremendous accuracy; and since the development of the World Wide Web also in an increasing size at a rapid rate over a large distance. Common sources of online text data are Wikipedia entries, movie subtitles or newspaper articles, which can be contained into respective corpora for every language. A text corpus allows to capture the frequency of a word simply by counting the number of total occurrences (Quasthoff et al., 2006). Calculating the co-occurrence of two (or a sequence of) words in a context (e.g. a sentence) further addresses their direct association and semantic similarity on a quantitative level (Evert, 2005; Frank & Willems, 2017; Hofmann et al., 2011; McKoon & Ratcliff, 1992; Rapp, 2002).

In the approach of the present thesis, word frequencies, co-occurrences and the total lexicon size are extracted from the corpus. Based on these counts, the log-likelihood can be computed for every word pair (cf. Dunning, 1993, Quasthoff et al., 2006). Next, the log-likelihood value is tested on positive or negative correlation. A direct association is assumed for a positive correlation, only, as both words need to occur. Positive log-likelihood values >6.63, which equals a *p* value of 0.01 in the chi-square distribution, are again $\log_{10}$ transformed, while all other log-likelihood values receive an associative strength of zero (Hofmann et al., 2011, 2014). The semantic relation is quantified by counting the common direct associates of two words (Rapp, 2002).

In line with the classification of syntagmatic relationships by de Saussure (1916), a direct association is stronger for words that occur more often together than expected from their overall frequency. COFFEE and CUP, for example, are highly frequent words that often co-occur in sentences like *"He pours coffee into the cup"*. Hence, a prediction of how the sentence "*He pours coffee into the…*" might continue can be formed due to familiar co-occurrences up to this point (Frank & Willems, 2017). Accordingly, paradigmatic relations by the definition of de Saussure (1916) reflect the semantic similarity of two words, as the number of common associates translates into their shared features (**Fig. 1**; also see Rapp, 2002). Thus, the higher their feature overlap, the more reliably they can be exchanged without altering the content of a sentence. For example, SCALE and RANGE share many direct associations such as VALUE, DEGREE and MARGIN, which form a similar context for both words. The benefits of this computational approach lie in the generalizability across a whole population and the independency on performance during pre-tests to acquire associative norms (Hofmann et al., 2014). Moreover, co-occurrences include not only the top associations as usually captured by subject-reliant methods (McKoon & Ratcliff, 1992), enabling gradual relations to set up full-factorial designs.

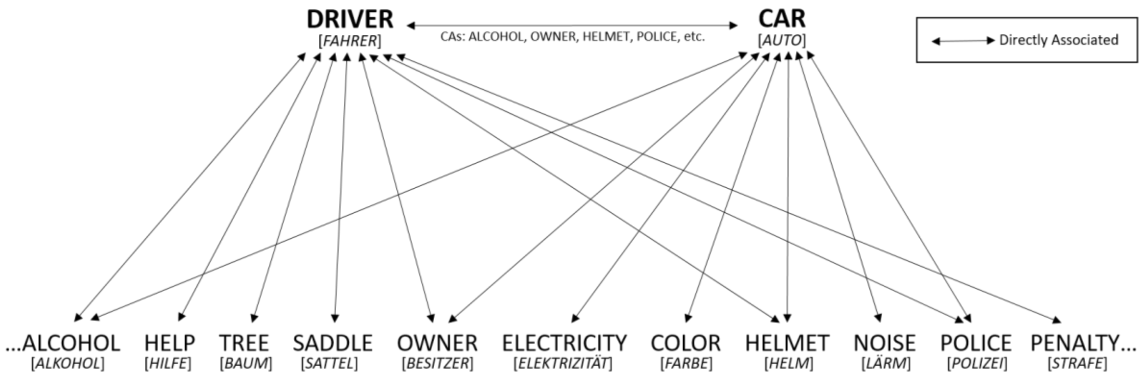

Fig. 1: *Depiction of the relationship of the words "driver" and "car". They are directly associated (bidirectional arrows) due to many co-occurrences like "The driver sits in his car". Both words also have a number of other direct associations, from which they share comparatively a lot: their common associates (CA).*

On the basis of word co-occurrences, neurocognitive models can predict the neural processing of words, paving a deeper understanding about the nature of language. One multilayer modelling approach, the Associative Read-Out Model (AROM), employs co-occurrences to simulate the interactive spread of neural activation for basic letter and word identification as well as semantic influences (Hofmann et al., 2011; Hofmann & Jacobs, 2014). **Fig. 2** shows the layering of the model.

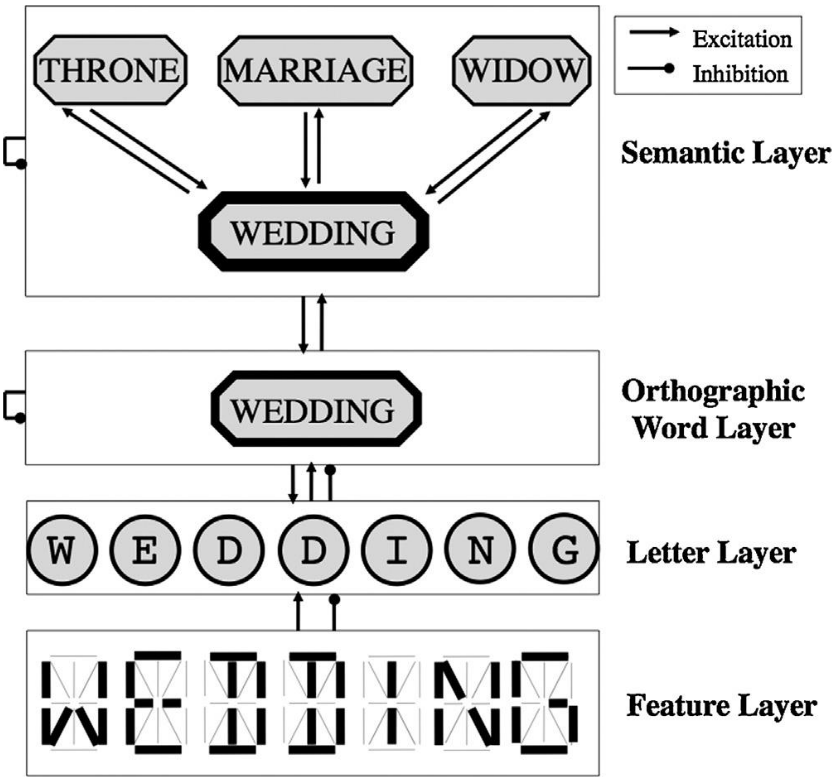

Fig. 2: *Architecture of the Associative Read-Out Model (AROM). Adapted from Hofmann and Jacobs (2014).*

The first three layers (feature, letter, orthographic) are identical to a classic interactive activation model (IAM) of word recognition (e.g. Grainger & Jacobs, 1996; McClelland & Rumelhart, 1981). Presenting a stimulus like WEDDING activates the corresponding single features of every letter on the lowest level. Next, the entire letters become activated, which in turn conform to the orthographically correct word. Connectivity between the nodes of a layer, and from one layer to another, can be inhibitory or excitatory. The letter “I”, for example, reduces the activation of any horizontal or diagonal feature but increases the input value of a vertical feature. Top-down feedback from the orthographic to the letter layer further enhances the correct identification of a contained character. By following these cognitively plausible rules, IAMs can predict influences of word length, frequency and orthographically similar words on response times and error rates (Cohen et al., 1990; Grainger & Jacobs, 1996; Jacobs et al., 1998). Semantic effects on visual word recognition, however, remained a black box for IAMs since their first proposal, leaving them with a rather poor performance on explicit recognition memory tasks (Gallo, 2013).

In recognition memory tasks, participants are asked to study items like words, and to later recollect them. The task difficulty can be further manipulated by the associative or semantic cohesion, which describes the number of directly associated or semantically related stimuli in the set, respectively. In the study phase, one half of the words are strongly related with each other (= high associative / semantic cohesion) while the other half is unrelated. In the subsequent test phase, unlearned words with an either strong or weak cohesion are added, requiring the participants to decide whether a presented word was previously studied or not. A strong cohesion within the stimulus set results in significantly more positive judgments for studied words, but also in a lot of false positives among the newly presented words (Hofmann et al., 2011; Roediger & McDermott, 1995; Stuellein et al., 2016). To account for such relationships can therefore be critical for the performance of an IAM.

The extension by a semantic layer allowed the AROM to address semantic co-activations to facilitate or inhibit the recognition of a stimulus. The underlying principle is the spreading activation theory proposed and incorporated into a model by Anderson (1983), Collins and Loftus (1975) and Quillian (1967). They conceptualized a semantic network of word nodes with interconnections that resemble a direct association to each other. As shown in **Fig. 1**, a DRIVER but not the CAR itself can call for HELP. DRIVER and HELP are therefore directly associated, CAR and HELP indirectly via DRIVER. By processing a word or concept, directly associated neighbors in a semantic network become activated as well as more distant, indirect relations with decreasing effectiveness. Furthermore, multiple activations on a word sum up, while the overall activation decays after stimulus exposure. This explains the increased rate of correctly remembered words with a high semantic cohesion due to the accumulated activation. A newly presented word with a high semantic cohesion to the studied items, on the other hand, can easily trick the retrieval process into a false response. The semantic layer in the AROM reflects these assumptions by updating word activations and interactions on every processing cycle until that activation crosses a threshold. Hence, the review by Hofmann and Jacobs (2014) highlights the model's performance on explicit memory tasks by successfully predicting false memories, familiarity checks and recollection.

1.2 PRIMED LEXICAL DECISIONS

Implicit memory tasks like naming and lexical decision without the involvement of semantics have been tested on classic IAMs, already (e.g. Grainger & Jacobs, 1996; McClelland & Rumelhart, 1981). However, one of Hofmann and Jacobs (2014) main objectives was to provide a model for the influence of semantics on explicit and implicit memory tasks. To investigate implicit semantic processing, Meyer and Schvaneveldt (1971), as well as Neely (1977) introduced the primed lexical decision paradigm. In a lexical decision task, the participant is instructed to correctly identify a stimulus as a word or nonword. The nonword can consist of random letter strings (e.g. TRZUGK), complies with a valid orthography (e.g. BANCE) or is a pseudohomophone (e.g. WERK sounds like WORK). Especially nonwords which follow the rules of a language prove to be more difficult to discriminate from a true word, resulting in longer response times and more errors (McNamara, 2005). The quality of the nonwords can therefore be a critical factor requiring a careful experimental design, depending on which effects a researcher might be interested in.

Semantic priming refers to the usually very short presentation of a preceding prime word, followed by an either related or unrelated target stimulus to which a lexical decision has to be made (Neely, 1977). Hence, the explicit instruction is focused on lexicality rather than on the implicitly manipulated prime-target relation. According to the spreading activation theory, a strong relation between the prime (e.g. DRIVER) and target (e.g. CAR; **Fig. 1**) facilitates the recognition of the latter – called the priming effect. Significant priming effects vary from ~15 to ~60 ms (McNamara, 2005; Neely, 1977). They can occur even for a very short prime duration of less than 100 ms (Perea & Gotor, 1997). If the onsets of prime and target (= stimulus onset asynchrony, SOA) are 200 ms apart or shorter, automatic processing causes solely facilitative priming. Thus, activation spreads in the network to pre-activate the target without top-down control. In contrast, strategic priming emerges at longer SOAs (Neely, 1991). Importantly, strategic processes can be both, inhibitory and facilitative, and consist of two main components. On the one hand, the reader is able to create an expectancy of which word might occur by exploring their semantic network for links to the prime. If the expectancy is confirmed, the priming effect is positive, and vice versa. On the other hand, the reader might search for connections of the prime and target after seeing the target word, which again can have an either positive or negative effect on the target recognition (McNamara, 2005; Neely, 1991). This is the reason why unrelated primes tend to elicit more “nonword” responses when seeing the target, as participants often fail to find a semantic match. Another influential factor during strategic processing is the relatedness proportion, which refers to the number of trials with related prime-target pairs relative to unrelated trials. A high relatedness proportion results in enhanced facilitation or inhibition because of a shift in expectancy (de Groot, 1984; Neely et al., 1989). Similarly, the associative / semantic cohesion (number of stimuli in a set that are related to a single target word) can pose as an issue if it is not matched across the conditions: A target word preceded by an unrelated prime but with a high associative / semantic cohesion could still have been primed by previous trials; especially at short SOAs where conscious expectancy evaluation is not developed (Balota et al., 1992). The quality of priming also differs depending on the type of relation between prime and target. As mentioned in section 1.1, the relation of two words can be classified into direct association and semantic similarity (also see the reviews on priming by Hutchison, 2003; Lucas, 2000; McNamara, 2005). Priming effects based on direct associations are considered to increase as SOA increases, because of the continuous spread of activation. Target words with a high semantic similarity to the prime are typically facilitated at short SOAs but inhibited at long SOAs (Lucas, 2000; McNamara, 2005; Plaut & Booth, 2000). McNamara (2005) was unable to give a definite explanation for this phenomenon, but suggested that the semantic set created during automatic processing is purely facilitative for prime-target pairs with a high overlap in meaning (Becker, 1980; Neely, 1991). The conscious search for the target in the semantic network, on the other hand, causes a solely inhibitory effect. It is unclear, however, why direct associations are largely unaffected by such inhibitions at long SOAs.

In consequence of diverging priming effects for direct associations and semantic similarity, the collective term “semantic priming” seems to be a relic from a time where no distinction between the two types was made (see McNamara, 2005). Thus, the term might be misleading especially in the context of the present thesis. For that reason, the following text across sections refers to “associative priming” for priming by direct associations, and to “semantic priming” for priming by semantic similarity unless explicitly mentioned otherwise.

A common debate in the priming literature revolves around the issue whether associative and semantic priming are separable or interact with each other. The “purity” of both priming types was profoundly investigated by Hutchison (2003), Lucas (2000) and McNamara (2005), as many studies failed to find an answer (e.g. Lupker, 1984; Shelton & Martin, 1992). In her meta-analysis, Lucas (2000) revealed evidence for the existence of pure semantic priming but not for pure associative priming. McNamara (2005) pointed out that pure semantic relations are easily accessible by looking for categorically similar words, e.g. from taxonomic trees: Words like BIKE and CAR are connected by the generic term VEHICLE, and are therefore strong substitutes for each other. In contrast, associative relations are usually acquired by free association norms, in which participants are asked to name the first associated word that comes to mind (Hutchison, 2003; Lucas, 2000). However, such norms often capture strong associations with semantic influences (e.g. DRIVER – CAR). As consequence, Lucas (2000) concluded that associative priming is inseparable from and stronger than semantic priming, as it contains an additional boost by semantics. Hutchison (2003) emphasized some methodological flaws in Lucas’ (2000) review like the inclusion of unpublished studies, or studies that investigated auditory and visual stimuli. In his polished meta-analysis, Hutchison (2003) found indications of pure associative priming for mediate associations (e.g. STRIPE primes LION via their link TIGER). Such mediate associations do not fit into the definition of direct associations, however, and might be a very special case of priming. Some more recent studies were also able to distinguish associative from semantic priming for certain subtypes of associative relations or by using free association norms, which – as mentioned above – might not be free of semantic influences (e.g. Coane & Balota, 2011; Ferrand & New, 2003). At this point, STUDY A of the present thesis attempts to shed light into these inconclusive observations by utilizing computationally calculated word co-occurrences (see section 2.1 for more details). Those co-occurrences should offer a more generalizable definition of word relations, and might allow a distinction of associative and semantic priming.

1.3 THE BIOLOGICAL PLAUSIBILITY OF CONNECTIONIST MODELS

IAMs belong to the group of connectionist models with localist representations, reflecting the view that a concept of knowledge can be contained into a single symbolic unit (Bowers, 2002; Grainger & Jacobs, 1996; Hofmann et al., 2011; Hofmann & Jacobs, 2014; McClelland & Rumelhart, 1981; Page, 2000). For instance, the word CAR is represented by one unit in such a model, exchanging information with its neighboring word units at a predetermined degree of activation (cf. **Fig. 1**). Thus, CAR always activates DRIVER by the same amount, but remains calm to orthographically and semantically distant words like FLOWER. Accordingly, there exist lower level letter units for "C", "A", and "R" as well as subordinated units for every letter feature (cf. **Fig. 2**), which exert a summed up activation to the CAR unit. This allows exact predictions of long term memory and a transparent view on the simulations due to deterministic calculations (Hofmann & Jacobs, 2014). The concept of symbolic units was put into question concerning the biological plausibility, as neuroimaging data has shown that a population of neurons is activated for every object (Plaut & McClelland, 2010; Quian Quiroga et al., 2008; but see Quian Quiroga et al., 2009 for single-cell findings). In addition, the brain does not work truly deterministic with always identical outcomes, but includes stochastic decisions.

The alternative approach is a distributed representation of information, which has been implemented by the utilization of hidden units to introduce non-linearity between an input and output as apparent for learning (Rumelhart & McClelland, 1986). Here, no single node but a number of hidden units represent the word CAR, which is comparable to a collection of word defining features. Every hidden unit can respond to many words, while the combination of active hidden units differs between the words. The better the word CAR was learned during training of the artificial neural network, the more (unique) hidden units are represented by it. This corresponds to the neural behavior of forming activation clusters to a certain event, and allows some redundancy in case of a local brain lesion (Seidenberg & McClelland, 1989). But also distributed representations suffer from biologically implausible flaws. For one, the usually applied back-propagation algorithm returns activation changes to the input layer via the same connections, while neural synapses transmit unidirectionally. Moreover, the learning system has to be stable for what was learned and plastic to allow new learning at the same time, resulting in a stability-plasticity dilemma for current models with distributed representations (Bowers, 2002; Page, 2000).

In his contribution to the localist versus distributed debate, Roy (2011, p. 219) pointed out that also distributed representations in multilayer models inevitably connect to higher-level layers with symbolic units to allow a judgment on the training. He concluded that a "localist, symbolic representation of higher-level concepts is an inherent and necessary part of [distributed] connectionist models of hierarchical semantic knowledge". In Roy (2012, p. 1), he further argued that "the only difference between localist and distributed representation is whether individual units have meaning and interpretation or not", as lower level units of localist models practically correspond to using hidden units as representation of an entire word unit (cf. **Fig. 3**).

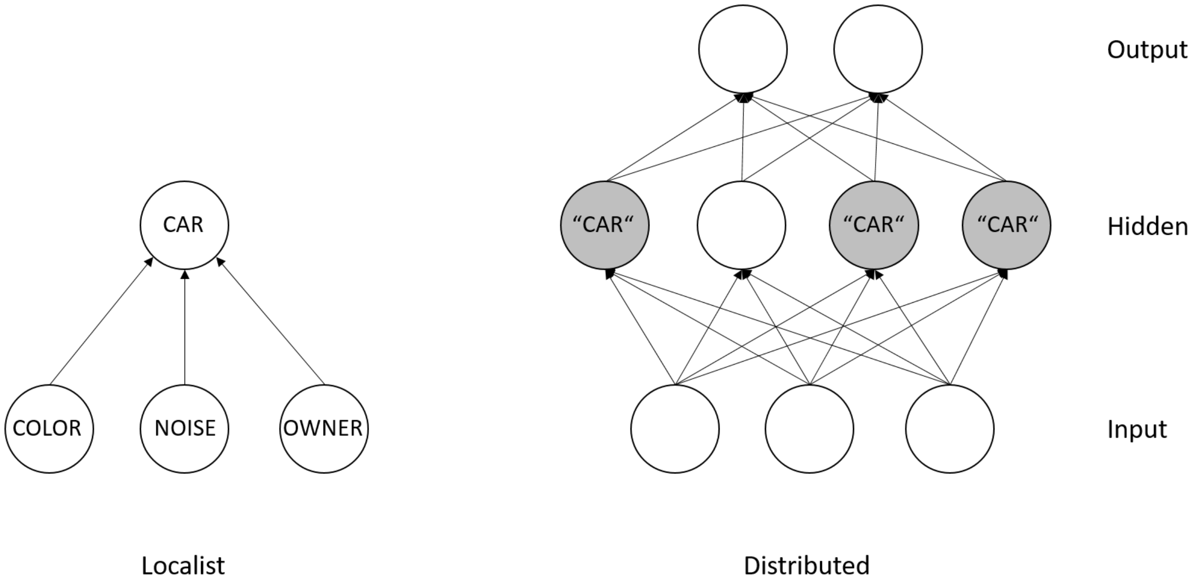

Fig. 3: *Simplified description of the difference between localist and distributed models. Localist models contain symbolic units for entire concepts like words. In distributed models, words are represented by an activation pattern of hidden units. For instance, three nodes in grey are active for the word CAR, which seems analogous to the symbolic units COLOR, NOISE and OWNER as features of CAR in a localist model.*

In sum, no current model can be entirely biologically plausible, but researchers should opt for a reliable foundation to account for behavioral and neuroimaging findings. Hence, the structure of the AROM is based on observations of visual word processing along the ventral visual stream to predict semantic processing (Hofmann & Jacobs, 2014; Mishkin et al., 1983).

1.4 THE SEMANTIC NETWORK AND FUNCTIONAL CONNECTIVITY ASSUMPTIONS BY THE AROM

The meta-analysis by Binder et al. (2009) revealed a left-lateralized semantic network of the fusiform gyrus, (anterior) middle and inferior temporal gyrus (MTG[1]), parahippocampus, inferior frontal gyrus (LIFG), prefrontal cortex, posterior cingulate cortex and the angular gyrus. They further pointed out that those regions appear to be heteromodal, thus unspecific to the quality of semantic information (shape, color, etc.). Of particular relevance for this thesis are the fusiform gyrus, MTG, parahippocampus, LIFG and the prefrontal cortex (**Fig. 4**), as they belong to the ventral visual stream of object processing, while the posterior cingulate cortex and the angular gyrus are part of the dorsal route to process spatial information (Hofmann & Jacobs, 2014; Mishkin et al., 1983).

In the case of visual word processing, the posterior fusiform gyrus receives single letter information from the occipital cortex and integrates them to an entire word; hence the term "visual word form area". The anterior fusiform gyrus is already involved into early semantic processing while being modulated by top-down influences from higher-level regions such as the parahippocampus and the MTG (Binder et al., 2009; Cohen et al., 2000; Kronbichler et al., 2004; McCandliss et al., 2003; Price, 2012; Vinckier et al., 2007).

The MTG was proposed by Patterson et al. (2007) as "semantic hub" to collect conceptual details like color, shape or orthography from distributed brain regions. This allows a semantic generalization across objects and their attributes. For instance, a pair of scissors and a knife are mostly used to cut or open something, but are different in their shape, handling and in which situation they are used for. Thus, it would be unusual to slice a bread with scissors. A hub region such as the MTG can acquire and bind the defining characteristics of an object or word to retrieve its entire semantic concept correctly. Evidence for a hub region originates from fronto-temporal disorders, which affect multiple modalities of semantic information (Patterson et al., 2007), resulting in e.g. slicing a bread with scissors.

The parahippocampus acts as interface between the semantic and hippocampal network to provide information about the semantic relation of two objects: Pattern completion highlights the semantic overlap to allow a generalization across items. In the example of scissors and knife, both are sharp, made of steel and are held in one hand. Pattern separation emphasizes distinct features such as consisting of two opposite blades versus one blade (Marr et al., 1991; McClelland et al., 1995; O'Reilly et al., 2014; Ranganath & Ritchey, 2012; Rolls, 2013; Yassa & Stark, 2011).

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[1] The literature often reports either the anterior temporal (e.g. Patterson et al., 2007) or the middle / inferior temporal gyrus (e.g. Binder et al., 2009) for responding to semantic retrieval processes. For reasons of simplicity, the present thesis refers to these functionally overlapping regions with the abbreviation "MTG".

The suppression of irrelevant semantic expectations is handled by the LIFG (Bedny et al., 2008; Sachs et al., 2011; Tivarus et al., 2006; Weber et al., 2016). As mentioned in section 1.2, it is critical for a correct recognition to quickly identify the target word among all pre-activated options by the prime. BREAD, for example, primes words like BUTTER, FLOUR and KNIFE, which all interfer with the target SCISSORS. This enhances LIFG activation to resolve any semantic conflicts. In this regard, Binder et al. (2009) pointed out that the LIFG is not necessary for task completion, but it increases the efficiency of the semantic network.

The prefrontal cortex functions as executive top-down guidance during the retrieval of semantic information. Increased activation in this area often implies the co-activation of the anterior cingulate cortex (ACC), but also the right cerebellum for semantic error detection (BREAD followed by SCISSORS), and to regulate the amount of control exerted by the prefrontal cortex. (Bedny et al., 2008; Binder et al., 2009; Botvinick et al., 2001; Hofmann et al., 2008a; Kringelbach, 2005).

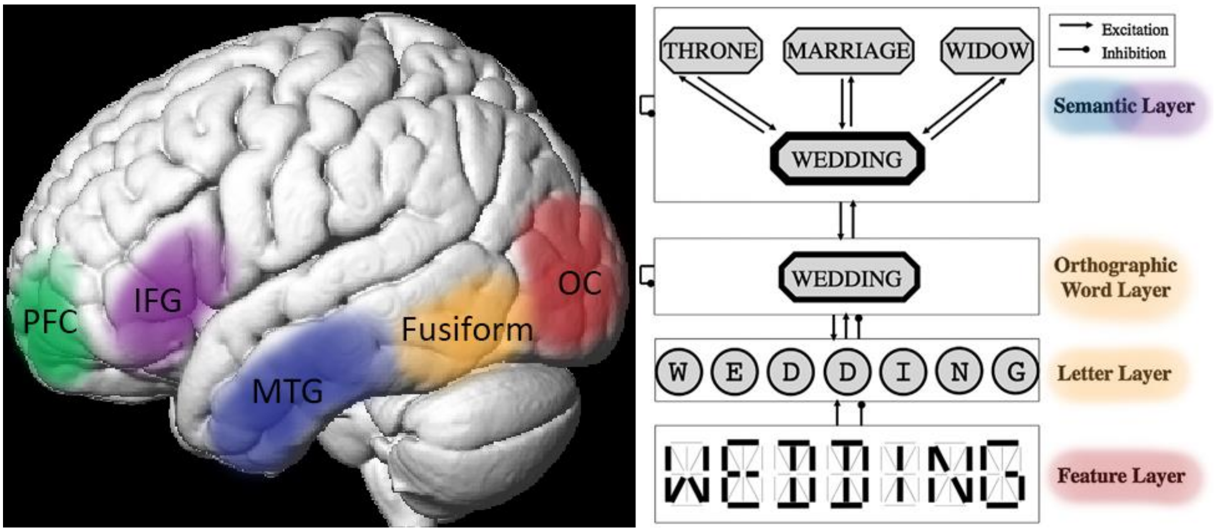


Fig. 4: *Regions of the semantic network (following Binder et al., 2009) and their proposed representation in the AROM (Hofmann & Jacobs, 2014). OC = Occipital cortex; MTG = (Anterior) middle / inferior temporal gyrus; IFG = Inferior frontal gyrus; PFC = Prefrontal cortex.*

Section 1.3 introduced the localist approach to illustrate neural connectivity during visual word processing from single features to letters and words. Addressing the biological plausibility of the AROM, Hofmann and Jacobs (2014) related the architecture of the model to regions in the ventral visual stream (**Fig. 4**). They suggested that letter features are processed in the occipital cortex, as the visual cortex (V1) contains neurons, which respond selectively to stimulus orientation (Hubel & Wiesel, 1962). Those features are integrated into letters and finally words most likely by the posterior fusiform gyrus (Cohen et al., 2000). This two-staged process is represented in the AROM by the letter and word layer. The semantic layer reflects the semantic network as presented above by accounting for the function of the MTG and LIFG: Semantic retrieval and resolution of semantic conflicts, respectively. The function of prefrontal regions and the ACC is addressed by the choice of a decision criterion, for example to regulate the amount of required orthographic or semantic activation.

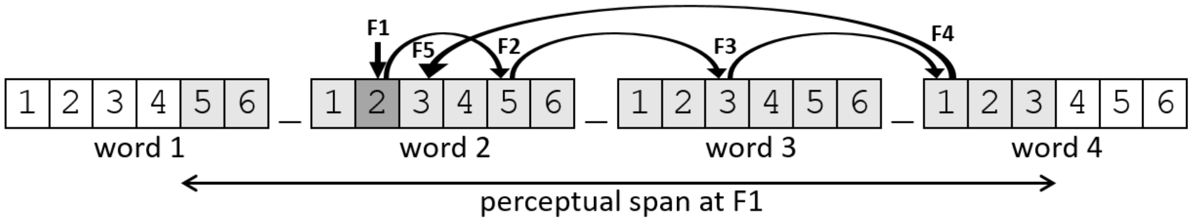
This intuitive and plausible structure of IAMs allowed researchers to readily predict brain activation. Botvinick et al. (2001) were able to explain activation in the ACC due to orthographic competition (e.g. MIST, FIST and LIST) by their model. Hofmann et al.'s (2008a) simulation data confirmed the involvement of the ACC with increasing event-related potentials in the N400/N2 components. With the implementation of the semantic layer, Hofmann and Jacobs (2014) further showed that co-occurrence-based direct associations can account for LIFG activation during the judgment of word familiarity. In an electroencephalography (EEG) study, Stuellein et al. (2016) observed an increased P200 amplitude for strong direct associations, thus at a similar time frame as the early lexical access (Hauk & Pulvermüller, 2004). This confirmed the proposed top-down feedback from the semantic to the orthographic layer by Hofmann and Jacobs (2014).

Most recently, Frank and Willems (2017) used co-occurrences for the quantification of direct association and semantic similarity to evoke diverging neural responses. They found increased activation in the fusiform gyrus, superior temporal gyrus and in the amygdala for low relative to strong direct associations. A low relative to a high semantic similarity resulted in more activation of the MTG, precuneus and the angular gyrus. Of note, they presented acoustic stimuli, which led to hemodynamic changes in regions that are more involved into phonological word processing such as the superior temporal gyrus (cf. Fig. 4 in Price, 2012). Yet, it creates a picture of how word co-occurrences can also address various associative processes for neuroimaging data. They concluded that direct associations elicit a top-down influence on the word forming process, similar to the findings by Stuellein et al. (2016). Semantic similarity, on the other hand, seems to account for activation in the semantic network. This further indicates that computationally calculated co-occurrences conform to the classic interpretation of associative and semantic relations. But how do these observations translate to visual word processing? And can the semantic connectivity assumptions by Hofmann and Jacobs (2014) be verified in a functional magnetic resonance imaging (fMRI) study that utilizes such word co-occurrences? STUDY B aims to provide answers to those questions (see section 2.2 for more details).

1.5 NATURAL READING BEHAVIOR

Models and empirical research on single word recognition offer a great opportunity to peek into the cognitive processes without contextual confounds. More usually in the daily life, one is confronted with whole sentences or entire paragraphs and books. Researchers commonly investigate lexical effects during natural reading by looking at the eye movement behavior. Fixations on a word last around 200 – 300 ms, while saccades from one fixation to the next take 30 – 50 ms (Rayner, 1998). For left-to-right reading, the area of effective vision (perceptual span) is constrained to 4 letters to the left and up to 15 letters to the right from the current fixation (Radach & Kennedy, 2013; Rayner, 1998). The following fixation is usually located within the perceptual span, hence in the parafoveal part of the visual field (Radach & Kennedy, 2013). Moreover, the first letters of a word contain the most important information for processing, resulting in an optimal viewing position slightly left from the center of a word (Bruner & O'Dowd, 1958; Hyönä et al., 1989; O'Regan, 1987; Rayner, 1998; Vitu et al., 2001).

Analysis of the first fixation duration on a word is most common in the literature as it reveals effects of early lexical and pre-lexical processing (Radach & Kennedy, 2013). Further measures include single fixation duration (only one fixation in total was needed to complete word processing), gaze duration (sum of all fixation durations until leaving the word captures a later stage of processing) and total viewing duration (sum of all fixation durations on a word, containing re-fixations to potentially cover top-down driven effects; see **Fig. 5** for an overview). Analyses can also focus on eye movements against the reading direction (regressions), word skipping, the landing position on a word and the (launch) distance between the last fixation and the beginning of the fixated word (Radach & Kennedy, 2013; Vorstius et al., 2014).



first fixation duration of word 2: F1
gaze duration of word 2: F1+F2
total viewing duration of word 2: F1+F2+F5
regression on word 2 from word 4: F5
single fixation duration of word 3: F3

Fig. 5: *Overview of eye movement behavior during reading and its parameters. F1 – F5 correspond to the subsequent fixations on the words. For reasons of simplicity, all words consist of six numbers 1 – 6.*

Word length, frequency and predictability are the most determining factors for how long and how often a word is fixated. Words with many letters, a low frequency and a low predictability result in more fixations, an increased fixation duration and less skipping. In addition, regressive eye movements are performed more likely to short words as they are skipped more frequently. Infrequent and unpredictable words are also more often the target of regressions to confirm previous processing or to repair insufficient processing (Himmelstoss et al., 2019; Inhoff & Rayner, 1986; Kliegl et al., 2004; Reichle et al., 2003, 2009).

Time course analyses revealed word length effects as early as 90 ms after stimulus presentation, thus during the word forming process (Assadollahi & Pulvermüller, 2003; Calvo & Meseguer, 2002; Hauk et al., 2006; Kliegl et al., 2004). 110 – 145 ms after fixation onset, bottom-up driven word frequency effects emerge (Himmelstoss et al., 2019; Kliegl et al., 2004; Reingold et al., 2012), which may interact with word length: Assadollahi and Pulvermüller (2003) reported frequency effects on short words in the range of 120 – 170 ms, and on long words much later at 225 – 250 ms; hence the increased fixation duration for long, unfamiliar words. Predictability effects mostly unfold at a very late top-down driven processing stage of 200 – 250 ms, when contextual information can be retrieved to make a prediction. This is reflected by larger effects in the analyses of regressive eye movements or the total viewing duration (Calvo & Meseguer, 2002; Himmelstoss et al., 2019; Kliegl et al., 2004; Rayner et al., 2004).

One would also assume early predictability effects in particular for infrequent words, as context predictions may facilitate their processing. High frequency words, on the other hand, should benefit less from such predictions due to their a priori likeliness to occur in the sentence (Kretzschmar et al., 2015). A temporal overlap in processing word frequency and predictability was observed by Sheridan and Reingold (2012), revealing a predictability effect already at 140 ms. They discussed that both lexical properties might still be processed independently from each other, as numerous studies failed to find statistical evidence for an interaction (e.g. Kliegl et al., 2004; Kretzschmar et al., 2015; Rayner et al., 2004; Staub, 2015). Few studies, however, found interactive effects of word frequency and predictability under certain conditions (e.g. Hand et al., 2012; Sereno et al., 2018). Hand et al. (2010) showed that predictability interacted with frequency, when the distance between the target word and the preceding fixation was short to medium. At a long launch distance, the interaction vanished. This would suggest that (interactive) lexical information of the target word can be processed already during a near pre-target fixation. However, Slattery et al. (2012) criticized the methodology of using launch distance as uncontrolled post-hoc factor, which could result in an imbalanced number of data points for each condition. Moreover, it was discussed that the interaction could have resulted from floor and ceiling effects due to oculomotor limitations. In another study, Sereno et al. (2018) manipulated the preview of the target word (valid/invalid) via the boundary paradigm. For an invalid preview, the target word was scrambled in the parafovea, denying any possible lexical pre-processing of that word.

Frequency and predictability interacted with each other at a valid preview, only. In the early measures of first fixation duration and single fixation duration, they found a frequency effect for words of low and medium predictability (with longest fixation durations on infrequent and unpredictable words) but not at a high predictability. They concluded that predictability effects can occur at very early stages of word processing to create an expectation of upcoming words. If the expectation is not met and the target word is also of low frequency, cognitive resources are pushed to their limit for a successful recognition.

To investigate early lexical effects, researchers also look at the influence of the target word (N) on the fixated preceding word (N-1) in a sentence – the parafoveal-on-foveal effect (PoF; see e.g. Radach & Kennedy, 2013; Schotter et al., 2012 for a review). PoF effects are generally accepted for sublexical and orthographic processing, but are under debate for lexical properties due to inconsistent findings – especially if they are under experimental manipulation (Angele et al., 2015; Schotter et al. 2012). In theory, most people would expect the sentence *"He took a nip from his cup, which contained hot…"* to finish with one of the frequent words WATER, TEA, MILK or COFFEE, but not with the high frequency word LIGHT. The presence of a predictability-dependent PoF effect would imply that the unpredictable word LIGHT had an effect on the currently fixated word HOT by modulating its first fixation duration (Hand et al., 2010; Hawelka et al., 2015; Kliegl et al., 2006; Snell et al., 2018). Accordingly, showing an unpredictable but also low frequency word like YEAST could potentially cause an interactive PoF effect of the two lexical properties (cf. Sereno et al., 2018). Utilizing the boundary paradigm on the second next word, Radach et al. (2013) even observed an N-2 PoF predictability effect if N-1 was a short and high frequency word, like HOT in the example above. Coming from N-2, they found increased skipping of N-1 if N was of high predictability. This indicates that lexical properties of COFFEE can influence the saccade planning while fixating the second last word CONTAINED.

Angele et al. (2015) and Schotter et al. (2012) criticized that many studies, which found lexical PoF effects, analyzed corpus data with uncontrollable linguistic influences (e.g. Hawelka et al., 2015; Hohenstein et al., 2010; Kliegl et al., 2006; but see Radach et al., 2013 for an experimental manipulation). They further argued that predictability-related PoF effects might not emerge from the word N, but that the effects on N-1 are generated from the preceding context (called successor effect). In the latter case, such effects should occur even when N is masked, which was reflected by Angele et al.'s (2015) results. Thus, they advocate a discrimination of true PoF effects and successor effects when interpreting eye movement data.

In regard to this controversy, Rayner and Schotter (2014) investigated whether letter capitalization, as apparent in e.g. German language, has resulted in many positive observations for lexical influences from the parafovea, while mainly English studies failed to find such effects. They manipulated the capitalization of a target noun in English sentences and reported a semantic preview benefit for capitalized words, only. This indicates that capitalization may draw attention to the parafoveal word earlier, allowing its processing already at a late stage of the currently fixated word.

All these observations led to diverging attempts to model eye movement behavior, which is addressed in the following section.

1.6 MODELS OF EYE MOVEMENT CONTROL

The aforementioned debate on interactive lexical effects and lexical PoF effects had consequences for the implementation of eye movement behavior into a computational framework. In general, there are two types of models, which mainly differ in how attention is allocated at the fixation of a word: Sequential attention shift (SAS) models and processing gradient (PG) models.

SAS models, like the E-Z Reader (Reichle et al., 2003, 2009), assume that attention is limited to a single word and moves in serial order to the following words. Concerning the biological plausibility, attention on one word ensures the correct collection of object information from different modalities. Moreover, it keeps the temporal order of word recognition in a sentence (first word 1, then word 2, then word 3, etc.). Among others, the model can predict saccade planning, word skipping, lexical influences and regressive eye movements. The implementation of regressions was criticized lately, as they are triggered selectively and are not based on context probabilities (Snell et al., 2018). Further criticism involves the handling of interactive lexical effects and lexical PoF effects, which seem to be elusive but observable (see section 1.5). At first glance, modelling a serial processing of words contradicts with the view of parallel processing of multiple words. Recently, Schotter et al. (2014) provided an update of the E-Z Reader and showed that their model can indeed account for this phenomenon. In its latest version, the model consists of two stages L_1 and L_2. L_1 represents early lexical processing of the fixated word N, after which saccade programming to the next word N+1 is initiated. At the same time of saccade planning, L_2 continues for later lexical processing of N. When L_2 of N is finished, attention moves to N+1 to allow some preview, before a saccade to that word is performed. That way, lexical PoF effects can occur, but are very dependent on the processing difficulty of N. A more difficult word N would lead to less or no PoF effects because of an increased duration in L_2 of N. Moreover, Schotter et al. (2014) admitted that the model addresses early stages (L_1 of N+1) of parafoveal preview, while it remains largely silent to late top-down influences from N+1 (L_2 of N+1). The coding of the model further assumes that frequency and predictability contribute to the processing time independently (cf. Equation 1 in Reichle et al., 2009). Thus, any evidence for their interaction would challenge the current implementation of the model (e.g. Hand et al., 2010; Sereno et al., 2018).

In contrast to SAS models, PG models propose that attention is distributed across the perceptual span as a gradient. The foveally perceived word receives the most attention, which is gradually reduced for parafoveally detectable words (Engbert et al., 2005). Parallel processing of more than one word is therefore directly included. Prominent PG models are the SWIFT model (Engbert et al., 2005), the Glenmore model (Reilly & Radach, 2006) and the OB1-reader (Snell et al., 2018). SWIFT allows similar predictions as the E-Z Reader, while also addressing target selection of regressive eye movements more realistically by looking at the activation level of the surrounding words instead of the inflexible hardcoding in the E-Z Reader. The Glenmore model is an IAM that performs already at the letter level. Hence, the activation gradient affects all perceivable letters, which sum up to the activation of the words. Criticism on those two models, and on PG models in general, mainly includes that words would not be recognized in a syntactically correct order due to the parallelism (Snell et al., 2018). The OB1-reader utilizes the PG structure and adds a spatiotopic sentence-level representation, which keeps track of the word order on a superordinate level. First, bigrams (a combination of two letters) of words in the perceptual span are activated, which in turn activate the word units. This is followed by a syntactic integration of all perceivable words to finally determine the next saccade target (the most salient word in the direction of reading versus a regression to an unrecognized word left from the current fixation; Reilly & Radach, 2006).

1.7 COREGISTERING EYE FIXATIONS TO NEUROIMAGING DATA

While the analysis of eye movements leaves some open questions regarding lexical influences, researchers recently started to align word fixations in sentences to neural responses in the brain. This fixation-related neuroimaging approach allows an ecologically more valid setting to peek into the cognitive processes than the previously often utilized rapid serial visual presentation (RSVP) of single words.

RSVP studies present words of a sentence one by one at a duration of 200 – 300 ms, equal to the average fixation duration (Buchweitz et al., 2009; Dambacher et al., 2009; Himmelstoss et al., 2019; Hofmann et al., 2014; Rayner, 1998; Yarkoni et al., 2008). This reduces the demand on bottom-up mechanisms like saccade planning, as word skipping and regressive eye movements are not possible. In turn, predictive errors due to incomplete word recognition can increase, which seems to engage (orbito-)frontal regions for a top-down regulation (Himmelstoss et al., 2019; Hofmann et al., 2014; Kiebel et al., 2008; Murray et al., 2014; Roesch & Olson, 2005). Moreover, PoF effects can only be tested under artificial conditions, e.g. by providing flankers: The previous word is shown on the left and the next word on the right, while the central word is replaced by the right word at a fixed pace (see Fig. 2 in Himmelstoss et al., 2019 for more details).

Word fixations during natural reading have been coregistered with EEG (e.g. Degno et al., 2019; Kretzschmar et al., 2015) and fMRI data (e.g. Schuster et al., 2016; 2020). Here, the onset of a fixation is used as marker for event-related potentials or hemodynamic responses, respectively (Dimigen et al., 2011; Hutzler et al., 2007; Marsman et al., 2012; Richlan et al., 2014). There have been concerns about the deconvolution of overlapping signals, as fixation durations are usually shorter than a) the investigated time window of 400 ms (N400) for lexical effects in EEG analyses or b) the slow dynamics of the blood oxygenation level dependent (BOLD) signal in fMRI analysis (Himmelstoss et al., 2019). As a result, fixation-related EEG studies struggle to distinguish frequency from predictability effects in the N400 component, even when the recorded eye movement data revealed main effects for both factors (Degno et al., 2019; Kretzschmar et al., 2015). Kretzschmar et al. (2015) interpreted the temporal overlap of frequency and predictability effects in the EEG data as evidence for their interaction on a cognitive level. Fixation-related fMRI studies are challenged by BOLD signals peaking ~6 seconds after stimulus exposure, because of their nonlinear interaction for fast-paced events like reading the words of a sentence (Binder et al., 1994; Friston et al., 1998; Huettel & McCarthy, 2000; **Fig. 6**). Still, distinct activation patterns for word frequency and predictability were observed by Schuster et al. (2016). A low frequency word elicited increased neural responses in the left fusiform gyrus, the LIFG, the ACC, the hippocampus and in the superior parietal cortex. The comparison of unpredictable and predictable words revealed relatively weak but hypothesis-driven effects for an uncorrected *p* value threshold of

0.05. Unpredictable words resulted in increased activation of the bilateral middle to superior temporal cortex, the LIFG, the orbitofrontal cortex (OFC) and the left fusiform gyrus. The authors related the small neurocognitive effects for word predictability to the also comparably weaker effects of predictability in the eye movement data (c.f. Kliegl et al., 2004).

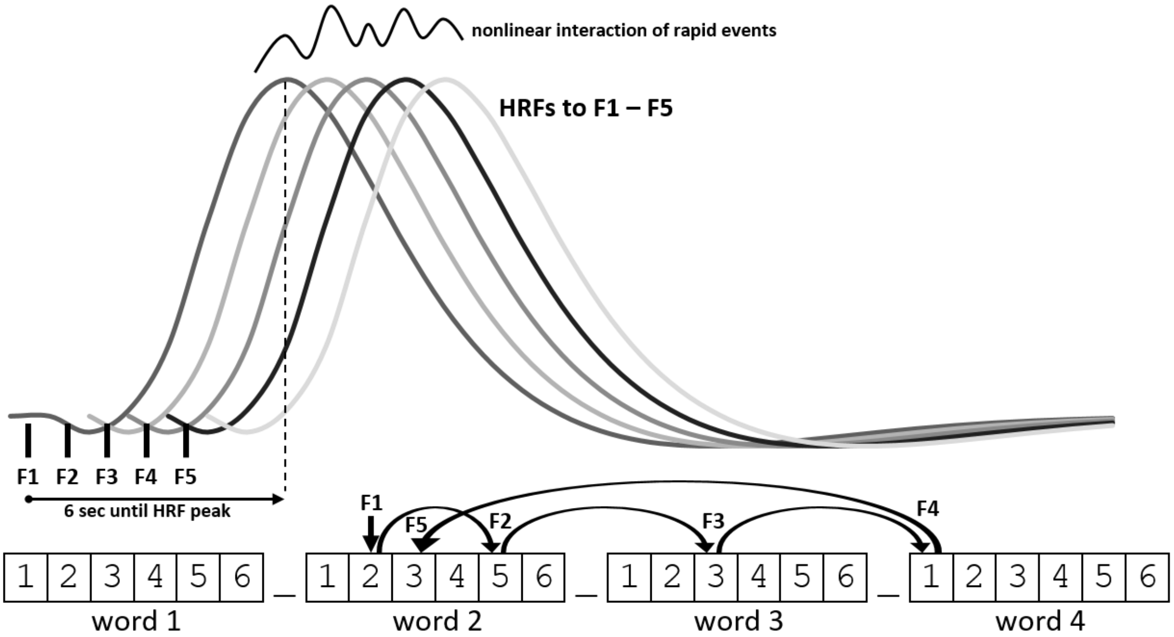


Fig. 6: *Schematic display of the coregistration of eye fixations (F1 – F5) and fMRI data. The hemodynamic response function (HRF) peaks ~6 sec after the fixation onset, and interacts in nonlinear fashion for multiple fast occurring events. For reasons of simplicity, all words consist of six numbers 1 – 6.*

While fixation-related EEG data seems to be silent not only to standard frequency effects, but also to lexical PoF effects (cf. Degno et al., 2019), Schuster et al.'s (2016) fMRI data indicates their existence. The left posterior MTG was activated stronger prior to a skipped word. Considering the involvement of the temporal cortex into higher order lexical processing, they suggested that lexical information from the next word was accessed already during saccade planning. In addition, also activation in the occipital cortex increased before skipping. Free visual exploration studies have shown that extrastriate regions guide the preparation of saccades (Larsson & Heeger, 2006; Mazer & Gallant, 2003; Merriam et al., 2007; Nakamura & Colby, 2000; Saber et al., 2015). It is therefore possible that lower level areas already use parafoveal lexical information to modulate the next saccade.

STUDY C picks up on the current state of fixation-related neuroimaging to investigate lexical PoF effects during natural reading. For the first time, it combines eye movement behavior with data from functional near-infrared spectroscopy (fNIRS), which allows a fast sampling of changes in hemodynamics (see section 2.3 for more details).

2 OVERVIEW AND METHODOLOGY OF THE PRESENT RESEARCH ARTICLES

2.1 INTRODUCING STUDY A: A NOVEL CO-OCCURRENCE-BASED APPROACH TO PREDICT PURE ASSOCIATIVE AND SEMANTIC PRIMING

The sheer complexity of visual word recognition entailed McNamara's (2005, p. 86) challenge for "anyone to find two highly associated words that are not semantically related in some plausible way". Lucas (2000, p. 627) further concluded that "purely semantic relationships are the best predictors of priming", and questioned the validity of spreading activation models due to their dependence on direct associations. STUDY A addresses those two statements, as word co-occurrences should provide a directly testable quantification of the amount of direct association and semantic similarity. The *deNEWS* corpus (version 2011) of the Leipzig Wortschatz Project, which consists of 70 million sentences and 1.1 billion words (Goldhahn et al., 2012), was used to compute word co-occurrences (see section 1.1 for more details). The corpus was pre-processed by transforming all words into lowercase and by removing any special characters. For the calculation of the semantic overlap, the one hundred most frequent words from the corpus were excluded, as they consisted of context-free stop words like THE, DO, or ARE.

The study applied a full-factorial manipulation of direct association (strong/no) and common associates (many/no) to investigate effects of pure associative and semantic priming. An independency of the two priming types would further suggest an additive (instead of an interactive) priming effect for word pairs with both, a strong direct association and many common associates. In other words, pure associative priming and pure semantic priming should sum up to the combination of both. Therefore, another goal of STUDY A was to compare the amount of priming elicited by any combination of the two factors.

In addition, the SOA of the prime and target was manipulated to be either short (200 ms) or long (1,000 ms) to evoke automatic and strategic processing, respectively. A strong direct association should lead to enhanced priming as SOA increases, because of the accumulated activation spread in the semantic network. Primes with many common associates should facilitate the target recognition at a short SOA, only, due to increased semantic competition at longer SOAs. Such an outcome would provide evidence that the co-occurrence approach can account for standard findings of associative and semantic priming at both SOAs.

2.2 INTRODUCING STUDY B: FUNCTIONAL CONNECTIVITY OF THE LEFT INFERIOR FRONTAL GYRUS DURING SEMANTIC PRIMING

STUDY B is an fMRI study that follows the goal to provide empirical evidence for the connectivity assumptions of the AROM concerning semantic processing. According to Hofmann and Jacobs (2014), the main target regions for representing the semantic layer are the LIFG and the MTG (**Fig. 4**). Prior fMRI research on semantic priming revealed that the LIFG is activated to resolve semantic conflicts when the prime and target are unrelated (Copland et al., 2007; Sachs et al., 2011; Tivarus et al., 2006; Weber et al., 2016). Activation of the MTG was also under investigation by researchers, but proved to be elusive when relying on the fMRI methodology due to a bad signal-to-noise ratio in that area (Bedny et al., 2008; Patterson et al., 2007; Sachs et al., 2011). Moreover, it was discussed that the temporal cortex sparsely responds to semantic competition, hence serving more as hub for semantic information (Bedny et al., 2008; Patterson et al., 2007). Therefore, STUDY B focused on the LIFG and its functional interaction in the semantic network.

To observe the functional connectivity between brain regions, this study employed psychophysiological interaction (PPI) analyses. After performing a standard group level ANOVA on neuroimaging data, one can manually define a “seed” region of interest (here the LIFG), that showed increased activation to a specific condition (e.g. an associative or semantic relation). Next, PPI analysis reveals all areas with a functional relation to the seed region. The direction of information flow, however, is not calculated by PPI. Some but possibly not all regions with significant effects in the group level ANOVA might also be functionally connected. For instance, the occipital cortex and the LIFG should both respond to the visual presentation of words. They are, according to the structure of the AROM however, not in direct functional interaction, as the occipital cortex contains “simple” feature information and the LIFG is involved into higher level semantic processing. On the other hand, the LIFG and the parahippocampus might directly exchange information about the semantic overlap of two words. Moreover, brain areas might not reach the significance threshold in the group level analysis, but can reveal an effect in the PPI analysis due to a strong coupling to the seed region (O’Reilly et al., 2012).

Recent research on PPIs during semantic processing indicated connectivity patterns along the ventral visual stream. Jackson et al. (2016) used PPIs in a semantic judgment task, in which participants had to choose one of two words that were semantically most similar to a prime. With the MTG as seed region, they reported a functional dependence to the LIFG, prefrontal gyrus, fusiform gyrus and the occipital cortex. In Weber et al. (2016), the LIFG further showed connectivity patterns to the ACC and the fusiform gyrus, when deciding between an animal word and a non-animal word.

To the knowledge of the author, no other published research has investigated PPIs with the LIFG as seed region for an implicit semantic memory task, so far. Thus, the novel aspects of STUDY B include a) the utilization of word co-occurrences to allow a direct linkage from model-to-brain-data, and b) a primed lexical decision task to investigate functional interaction effects on implicit semantic memory.

2.3 INTRODUCING STUDY C: FIXATION-RELATED NIRS INDEXES RETINOTOPIC OCCIPITAL PROCESSING OF PARAFOVEAL PREVIEW DURING NATURAL READING

The elusiveness of lexical PoF effects and interactive effects of word frequency and predictability resulted in the discussion, whether readers process words sequentially or in parallel (cf. Reichle et al., 2009; Snell & Grainger, 2019). Thus, eye movement research has recently adopted the simultaneous acquisition of neuroimaging data. While the findings of fixation-related EEG were sparse even for standard frequency effects (Kretzschmar et al., 2015; Degno et al., 2019), fixation-related fMRI data revealed first indications of lexical influences by the following word on the currently fixated word (Schuster et al., 2016).

To provide further insight on this topic, STUDY C utilized the high sampling frequency of an optical imaging technique, fNIRS, to investigate hemodynamic changes similar to fMRI. fNIRS is a non-invasive method that takes advantage of the differences in light absorption of oxygenated hemoglobin [oxy-Hb] (stronger absorption at ~850 nm) and deoxygenated hemoglobin [deoxy-Hb] (stronger absorption at ~760 nm; Ye et al., 2008). Light emitting optodes (sources) and signal receiving detectors are placed on the skull to cover the areas of interest. When near-infrared light is transmitted through the skull, some parts are absorbed by the hemoglobin, while the scattered remainder can be captured by the detectors. This banana-shaped flow of light from the source to the detector generally refers to the term “channel”. The inherent consequence of this light based method is the restriction to the top 15 mm of the cortex due to the skull thickness (Gervain et al., 2011; Quaresima et al., 2011).

An increased neural activity is reflected by more [oxy-Hb] and less [deoxy-Hb], which allows the cross-validation of the cognitive demand during a task (Buxton et al., 2004; Hoshi et al., 2001). This serves as an advantage of fNIRS over fMRI, which covers [deoxy-Hb] (Glover, 2011). Moreover, fNIRS provides a much higher sampling rate, but at the cost of spatial resolution. Because of the nonlinearity of BOLD signals during rapid event successions (Binder et al., 1994; Friston et al., 1998; Huettel & McCarthy, 2000), more data points can provide a better dissection when reading multiple words every second. In addition, every word fixation includes several sub-processes such as orthographic and lexical integration, and saccade planning and execution, which might elicit distinct neural responses. While the spatial resolution is worse than for fMRI (but better than EEG), Tsuzuki et al. (2007) provided estimates for the relation of channel location to subregions of the cortex (http://www.jichi.ac.jp/brainlab/download/AP1005_anterior.xlsx). For instance, a channel between the O1 and PO7 optode position refers to the V3 region of the occipital cortex; a channel between O1 and Oz to the V2 region (see the methods of STUDY C and **Table 10** for more information).

The stimuli and the experimental design of STUDY C were identical to the study by Hofmann et al. (2014). Hofmann et al. (2014) investigated frequency and predictability effects via fNIRS by presenting sentences word-by-word (RSVP paradigm). Thus, no PoF effects were observable and saccade-driven bottom-up influences were reduced in comparison to self-paced reading. They experimentally manipulated the frequency and predictability of a target word, and looked at the impact on OFC and occipital activation. They found increased neural responses in the occipital cortex to unpredictable words, as no match for context based pre-activations was shown. Moreover, a predictability effect occurred in the OFC only if the word was infrequent. They concluded that, together with a false top-down prediction of the target word, a low frequency further reduced the available bottom-up information. This delayed the target word processing, while subsequent words continued to appear due to the RSVP paradigm. As a result, the OFC was activated to keep the timing of word processing in check (Kiebel et al., 2008; Murray et al., 2014; Roesch & Olson, 2005).

STUDY C focused on the same target regions as Hofmann et al. (2014), the occipital cortex and the OFC. Of first interest was the activation pattern in the OFC in relation to the lexical effects. At a self-paced reading rate with the option to perform regressive eye movements, it might not be necessary to regulate the order of word processing. Occipital cortex activation during free visual exploration was previously related to saccade preparation (Larsson & Heeger, 2006; Mazer & Gallant, 2003; Merriam et al., 2007; Nakamura & Colby, 2000; Saber et al., 2015). Therefore, it is likely that more difficult words (in the parafovea) delay the subsequent saccade, which could be evidence for lexical PoF effects (cf. Schuster et al., 2016). Because of the experimental manipulation of the target word, a positive result would correspond to a true PoF effect, and not a successor effect as discussed by Angele et al. (2015). Furthermore, an interaction between word frequency and predictability would indicate a parallel processing of the lexical properties.

3 RESEARCH ARTICLES OF THE DOCTORAL THESIS[2]

3.1 STUDY A

Table 1: *Bibliographic information of STUDY A.*

Title	**A novel co-occurrence-based approach to predict pure associative and semantic priming**
Authors and Affiliations	Andre Rölke-Wellmann[a], Nicole Franke[a,b], Chris Biemann[c], Ralph Radach[a], Arthur M. Jacobs[d,e,f], Markus J. Hofmann[a] [a] General and Biological Psychology, Bergische Universität Wuppertal, Germany [b] General Psychology (Judgment and Decision Making), Fernuniversität in Hagen, Germany [c] Language Technology, Universität Hamburg, Germany [d] Experimental and Neurocognitive Psychology, Freie Universität Berlin, Germany [e] Dahlem Institute for Neuroimaging of Emotion (D.I.N.E.), Freie Universität Berlin, Germany [f] Center for Cognitive Neuroscience (CCNB), Freie Universität Berlin, Germany
Publication Outlet	Psychonomic Bulletin & Review
Publication Type	Journal Article
Publication Year	2018
Publication Status	Published
DOI	https://doi.org/10.3758/s13423-018-1453-6
Abstract	The theoretical "difficulty in separating association strength from [semantic] feature overlap" has resulted in inconsistent findings of either the presence or absence of "pure" associative priming in recent literature (Hutchison, 2003, *Psychonomic Bulletin & Review, 10*(4), p. 787). The present study used co-occurrence statistics of words in sentences to provide a full factorial manipulation of direct association (strong/no) and the number of common associates (many/no) of the prime and target words. These common associates were proposed to serve as semantic features for a recent interactive activation model of semantic processing (i.e., the associative read-out model; Hofmann & Jacobs, 2014). With stimulus onset asynchrony (SOA) as an additional factor, our findings indicate that associative and semantic priming are indeed dissociable. Moreover, the effect of direct association was strongest at a long SOA (1,000 ms), while many common associates facilitated lexical decisions primarily at a short SOA (200 ms). This response pattern is consistent with previous performance-based accounts and suggests that associative and semantic priming can be evoked by computationally determined direct and common associations.

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[2] Adapted preprint versions of the published research articles.

3.1.1 INTRODUCTION

In a primed lexical decision task, one can broadly distinguish between associative and semantic priming (Hutchison, 2003). Semantic priming effects are primarily observed at short (<250 ms) stimulus onset asynchronies (SOAs; Ferrand & New, 2003; Lucas, 2000; McNamara, 2005). This dependence on SOA is caused by competing semantic information: While early processing is always facilitative, at a long SOA (>500 ms) the search for a semantic match leads to additional facilitation if the expectancy is met, interacting with inhibition by strong semantic competitors (Balota et al., 1992; Neely, 1977; Neely et al., 1989). Associative priming, in contrast, is based on rapid spreading of activation in the network, which continuously facilitates the recognition of a prime's neighbor at increasing SOAs (Hutchison, 2003).

While "pure" semantic priming can be obtained with great care, "pure" associative priming is widely dismissed due to the difficulty of diminishing the semantic similarity (Lucas, 2000; McNamara, 2005). However, Coane and Balota (2011) showed that words with recent direct or mediate associations reveal patterns of semantic priming even without any feature overlap. Ferrand and New (2003) further separated associative from semantic priming by using Alario and Ferrand's (1999) word association norms and semantic similarity ratings to rule out strong semantic relations in "purely" associated words (and vice versa). However, when predicting human performance by another human performance, such norms bear the risk of circularity (Hofmann et al., 2011). We think that this is problematic for the generality of a model (Hofmann & Jacobs, 2014), because free associations probably capture only a few of the most strongly associated words. Nowadays, co-occurrence-based approaches belong to the standard repertoire of researchers in the field of semantic processing (e.g. Andrews et al., 2009). Though none of these approaches systematically differentiated associative from semantic relations so far, computational linguistics provide an option for their dissociation: Word pairs can be defined as directly associated when they are more likely to co-occur in a sentence than predicted by their single occurrence frequency (Evert, 2005; Hofmann et al., 2011). This definition seems to perfectly resemble a "syntagmatic" relation (de Saussure, 1916). Rapp (2002) described higher order semantic similarity by the number of shared associates of two words (Hofmann & Jacobs, 2014; Stuellein et al., 2016). Hence, with increasing number of common associates, two words become categorically similar substitutes, resembling a "paradigmatic" relation (Rapp, 2002). This allows a fully transparent symbolic approach to semantics in an interactive activation modeling framework (Hofmann & Jacobs, 2014; McClelland & Rumelhart, 1981).

Consequently, the present study not only focused on isolating direct associations from semantic similarity but also on the effect of their combination. In a spreading activation network, one might assume additive and therefore independent (priming) effects of both factors on word recognition, as already shown for multiple convergent primes (Balota & Paul, 1996). Hence, we used a full factorial manipulation of direct association (strong/no) and the number of common associates (many/no) to test whether our four experimental conditions reflect the following conditions in the classic priming literature:

a) A strong direct association together with many common associates reflects semantic priming with an additive associative boost (*Associative+Semantic*; e.g. DRIVER – CAR).
b) Only a strong direct association resembles pure associative priming (*Associative*; e.g. COLD – HUNGER).
c) Only many common associates reflect pure semantic priming (*Semantic*; e.g. SCALE – RANGE).
d) Neither a direct association nor any common associates results in unrelated words (*Unrelated*; e.g. DATE – MOOSE).

We included SOA (200/1,000 ms) as an additional factor to test whether word pairs with a direct association elicit stronger (pure) priming effects at a long SOA. Many common associates, in contrast, should elicit (pure) semantic priming mainly at a short SOA due to semantic competition as SOA increases. Moreover, post hoc comparisons of *Associative+Semantic* versus the sum of *Associative* and *Semantic* priming should not differ significantly at both SOAs, which can be verified by JZS Bayes factor analysis (Rouder et al., 2009) to favor the null hypothesis (additive) instead of the alternative (overadditive).

3.1.2 METHOD

Two experiments with identical stimuli were conducted. While Experiment 1 was a behavioral study, Experiment 2 was carried out at the Center for Cognitive Neuroscience Berlin (Freie Universität Berlin; http://www.ewi-psy.fuberlin.de/en/v/ccnb/) on a Siemens Magnetom 3T TrioTim syngo MR B17 scanner with a 12-channel receiver head coil.[3]

In Experiment 1, 32 native German speakers (20 female, *M* = 26.69 years, *SD* = 5.14 years) participated in the primed lexical decision task, while the same number participated in Experiment 2 (20 female, *M* = 26.53 years, *SD* = 5.16 years). None of them reported language, psychiatric or neurological disorders. One participant of Experiment 2 had to be excluded from analyses because of brain damage in the temporal lobe during childhood. Participants were paid in cash or received course credits.

The stimuli consisted of 200 word-word pairs (25 per condition) and 200 word-nonword pairs. We selected words with a length of three to eight letters, a Leipzig word frequency class of seven to fifteen (Hofmann et al., 2011; Quasthoff et al., 2006), and a maximum of seven orthographic neighbors

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[3] As this study focusses on establishing a computationally derived approach for a full-factorial design of associative and semantic priming based on behavioral data, fMRI data is not further analyzed or discussed at this point (but see STUDY B).

(Grainger & Jacobs, 1996), and matched all the primes and targets in all four priming conditions on length, frequency class, and number of orthographic neighbors (all *F*s < 1; see **Table 2**). The direct associative strength was derived from a 43-million-sentences corpus consisting of more than 7.5 million word types by calculating the likelihood of all possible word pairs. All pairs with a likelihood value >6.63 were defined as directly associated (Hofmann et al., 2011; cf. Quasthoff et al., 2006). Matched across all conditions with a strong direct association, the log10 transformed prime-target likelihoods were selected to be top associates and ranged from 2.16 to 4.09 (*M* = 3.33, *SD* = 0.36), or in joint raw frequency from 16 to 1,781 (*M* = 405.99, *SD* = 371.53). The number of common associates of prime and target resulted from the sum of all shared associates (Quasthoff et al., 2006; Rapp, 2002). Matched across all conditions with many common associates, the stimuli were selected to have the largest number of shared associates ranging from 11 to 42 (*M* = 23.7, *SD* = 5.61). We ensured that no correlation between direct associations and common associates existed (*r* = .0092).

Table 2: *Mean values (standard deviation in parentheses) of the controlled variables.*

SOA	Condition	AS	CA	Letters Prime	FreqClass Prime	OrthNeighb Prime	Letters Target	FreqClass Target	OrthNeighb Target
200 ms	Associative+Semantic	3.28 (0.42)	25 (7.38)	5.48 (1.39)	11.24 (2.05)	1.84 (1.95)	5.72 (1.59)	11.28 (2.19)	1.4 (1.71)
	Associative	3.35 (0.28)	0 (0)	5.84 (1.31)	10.96 (2.07)	1.6 (1.76)	5.36 (1.08)	10.56 (1.87)	1.56 (1.61)
	Semantic	0 (0)	22.92 (4.01)	5.24 (1.36)	11.84 (1.89)	1.96 (1.99)	5.88 (1.01)	11.56 (2.42)	1.92 (1.89)
	Unrelated	0 (0)	0 (0)	5.52 (1.48)	10.84 (2.17)	2.04 (1.74)	5.32 (1.52)	11 (2.06)	1.96 (1.72)
1,000 ms	Associative+Semantic	3.29 (0.44)	23.08 (6.51)	5.64 (1.47)	11.24 (2.07)	1.76 (1.85)	5.48 (1.33)	10.64 (2)	2.08 (2.12)
	Associative	3.42 (0.24)	0 (0)	5.44 (1.47)	10.96 (1.86)	1.68 (1.91)	5.48 (1.29)	10.92 (2.47)	1.56 (1.47)
	Semantic	0 (0)	23.8 (3.75)	5.24 (1.51)	11.12 (2.2)	1.64 (1.82)	5.6 (1.58)	11.36 (2.43)	1.56 (1.76)
	Unrelated	0 (0)	0 (0)	5.44 (1.33)	11.24 (2.31)	1.64 (1.6)	5.88 (1.36)	11.24 (2.37)	1.64 (1.7)

Note. AS = (direct) associative strength; CA = number of common associates, number of letters, Leipzig frequency class, and orthographic neighbors, for prime and target in each condition.

The word-nonword pairs used a different set of prime words, which were unrelated with primes and targets of all word-word conditions and were matched with the primes of the word targets. The target nonwords were created by replacing two letters from the original target words (consonants and vowels from all positions equally often and in all variations). Half the nonwords followed the phonological rules of German language, while the other half consisted of unpronounceable random letter strings. We prepared 20 practice trials (half word-word pairs) with identical selection criteria as above.

In both experiments, participants were positioned within a standardized distance of ~70 cm from the screen. Each participant received a unique pseudorandomized order of stimuli with no more than three pairs with word (or nonword) targets in sequence. The stimuli were presented in uppercase and in a black font (Times New Roman) on a white background. A trial started with the presentation of the prime word (150 ms) at the center, followed by a blank screen for 50 ms or 850 ms, depending on the SOA. The target word was presented for 200 ms. Eight hash characters (########) replaced the target word until a response was given (1,300 ms maximum). Trials were separated by a centered fixation cross (+) for 1-10 s. Participants were instructed to focus on the fixation cross and respond as fast and as accurately as possible. Response times (RT) were recorded from target presentation until the subject's decision. RTs deviating more than three standard deviations from the mean RT per subject and condition were discarded. In addition, we entered the error rates (ERs) across all conditions into our analyses. The data of both experiments were merged into one analysis after ensuring that the factor Experiment (1/2) did not interact with any priming effects (RT: $F(2, 60) = 2.21$, $p = 0.118$, $\eta_p^2 = 0.069$; ER: $F(2, 60) = 0.28$, $p = 0.758$, $\eta_p^2 = 0.009$). *P* values of all post hoc comparisons were Bonferroni-corrected to reduce Type I errors.

3.1.3 RESULTS

3.1.3.1 RESPONSE TIMES

We first submitted the within-subject factors direct association (strong/no), common associates (many/no) and SOA (200/1,000 ms) to 2 × 2 × 2 ANOVAs (F_1: analysis by subjects; F_2: analysis by items). Main effects were found for direct association (strong: 662 ms vs. no: 695 ms; $F_1(1, 62) = 85.88$, $p < 0.001$, $\eta_p^2 = 0.581$; $F_2(1, 192) = 32.24$, $p < 0.001$, $\eta_p^2 = 0.144$), common associates (many: 670 ms vs. no: 687 ms; $F_1(1, 62) = 43.55$, $p < 0.001$, $\eta_p^2 = 0.413$; $F_2(1, 192) = 9.37$, $p < 0.01$, $\eta_p^2 = 0.047$) and for SOA (short: 691 ms vs. long: 666 ms; $F_1(1, 62) = 35.08$, $p < 0.001$, $\eta_p^2 = 0.361$; $F_2(1, 192) = 15.01$, $p < 0.001$, $\eta_p^2 = 0.072$). Subject analysis further revealed an interaction between direct association and SOA ($F_1(1, 62) = 6.55$, $p < 0.05$, $\eta_p^2 = 0.096$). *T*-tests showed that directly associated words induced a significant reduction of RT at both SOAs (short: 678 ms vs .703 ms, $t(62) = -5.42$, $p < 0.001$; long: 646 ms vs. 686 ms, $t(62) = -9.81$, $p < 0.001$) with significantly stronger effects at the long SOA ($t(62) = -2.56$, $p < 0.05$). In addition, we observed a significant interaction between common associates and SOA in F_1 ($F_1(1, 62) = 7.3$, $p < 0.01$, $\eta_p^2 = 0.105$): Many common associates resulted in a significant effect only at the short SOA (short: 678 ms vs. 703 ms, $t(62) = -6.23$, $p < 0.001$; long: 661ms vs. 671ms, $t(62) = -2.57$, $p = 0.052$). All other interactions were not significant.

Afterwards, we *t*-tested the priming effects *Associative+Semantic*, *Associative*, and *Semantic* for significance at both SOAs by computing the mean of the respective conditions per subject and subtracting the *Unrelated* condition (see **Table 3**). Pure *Associative* priming reached significance at both SOAs (short: $t(62) = 3.01$, $p < 0.05$; long: $t(62) = 8.16$, $p < 0.001$), increasing significantly as SOA increased ($t(62) = -2.65$, $p < 0.03$). Pure *Semantic* priming yielded a significant effect only at the short

SOA (short: *t*(62) = 2.95, $p < 0.05$; long: *t*(62) = 1.57, *p* = 0.726). *Associative+Semantic* priming was significant – and equally strong – at both SOAs, (200 ms: *t*(62) = 8.2, $p < 0.001$; 1,000 ms: *t*(62) = 8.21, $p < 0.001$).

Table 3: *Mean RTs (in ms) and % errors (% ER) and priming effects for RTs and % ER relative to the unrelated priming condition as a function of SOA (*p < .05). Standard errors are provided in parentheses.*

SOA	Effect	Associative	Semantic	Associative+Semantic	Unrelated
200 ms	RTs	693 (10.5)	694 (12.4)	662 (10.3)	713 (11.8)
	Priming	**20*** (6.6)	**19*** (6.4)	**51*** (6.3)	0 (0)
	%ER	4.4 (0.7)	5.5 (0.8)	2.4 (0.5)	6.5 (0.7)
	Priming	2.1 (0.8)	1 (0.7)	**4.1*** (0.7)	0 (0)
1,000 ms	RTs	652 (11.5)	682 (11.1)	640 (10.6)	690 (11.9)
	Priming	**38*** (4.7)	8 (5.1)	**50*** (6.1)	0 (0)
	%ER	5.1 (0.7)	6.3 (0.8)	2.6 (0.5)	5.1 (0.8)
	Priming	0 (0.7)	-1.2 (0.7)	**2.5*** (0.7)	0 (0)

To substantiate how pure *Associative* and *Semantic* priming interact with SOA, we submitted them to a 2 (type of pure priming: *Associative/Semantic*) × 2 (SOA: 200 ms/1,000 ms) ANOVA. While a main effect for pure priming occurred in F_1 ($F_1(1, 62) = 14.57$, $p < 0.001$, $\eta_p^2 = 0.19$; $F_2(1, 192) = 2.73$, $p = 0.102$, $\eta_p^2 = 0.028$) analysis by items showed a main effect for SOA ($F_1(1, 62) = 0.3$, $p = 0.586$, $\eta_p^2 = 0.005$; $F_2(1, 192) = 6.26$, $p < 0.05$, $\eta_p^2 = 0.061$). In addition, a significant interaction between the two factors was observed for subject analysis ($F_1(1, 62) = 14.1$, $p < 0.001$, $\eta_p^2 = 0.185$; $F_2(1, 62) = 2.6$, $p = 0.111$, $\eta_p^2 = 0.026$). *T*-tests revealed that pure *Associative* priming increased significantly at the long SOA (+18 ms; *t*(62) = −2.65, $p < 0.05$), while pure *Semantic* priming showed a nonsignificant decrease only towards the long SOA (−11 ms: *t*(62) = 1.23, *p* = 0.223). In addition, both priming effects did not differ at the short SOA (*t*(62) = 0.2, *p* = 0.846), but at the long SOA *Associative* priming was significantly stronger than *Semantic* priming (*t*(62) = 6.13, $p < 0.001$).

Then, we performed another 4 (type of priming: *Associative+Semantic/Associative/Semantic*/ Sum of *Associative* and *Semantic*) × 2 (SOA: 200 ms/1,000 ms) ANOVA by subjects to check for (over)additivity of *Associative+Semantic* priming by comparing it against the sum of *Associative* and *Semantic* priming: A significant main effect was revealed for priming types ($F_1(3, 62) = 41$, $p < 0.001$, $\eta_p^2 = 0.672$), but not for SOA ($F_1(3, 62) = 0.16$, $p = 0.69$, $\eta_p^2 = 0.003$). Moreover, the interaction of both factors was significant ($F_1(3, 62) = 6.23$, $p < 0.001$, $\eta_p^2 = 0.237$). While *Associative+Semantic* priming was significantly stronger than *Associative* and *Semantic* priming at the short SOA (*Associative*: *t*(62) = 7.11, $p < 0.001$; *Semantic*: *t*(62) = 5.88, $p < 0.001$), only *Semantic* priming was significantly weaker at the long SOA (*Associative*: *t*(62) = 2.31, *p* = 0.24; *Semantic*: *t*(62) = 7.33, $p < 0.001$).

In addition, *Associative+Semantic* priming did not differ significantly from the sum of *Associative* and *Semantic* priming effects at both SOAs (200 ms: $t(62) = 1.67$, $p = 0.6$; 1,000 ms: $t(62) = 0.5$, $p = 1$). Scaled ($r = .707$) JZS Bayes factor analysis (Rouder et al., 2009) showed that at both SOAs, the observed data was two to six times more likely under the additive (null) model (short: $BF_{01} = 1.95$; long: $BF_{01} = 6.43$).

3.1.3.2 ERROR RATES

The 2 (direct association: strong/no) × 2 (common associates: many/no) × 2 (SOA: 200 ms/1,000 ms) ANOVA of ER revealed a significant main effect for direct association ($F_1(1, 62) = 26.6$, $p < 0.001$, $\eta_p^2 = 0.3$; $F_2(1, 192) = 7.85$, $p < 0.01$, $\eta_p^2 = 0.039$) and by subjects for common associates ($F_1(1, 62) = 9.23$, $p < 0.01$, $\eta_p^2 = 0.13$; $F_2(1, 192) = 1.88$, $p = 0.172$, $\eta_p^2 = 0.01$) but not for SOA ($F_1(1, 62) = 0.09$, $p = 0.764$, $\eta_p^2 = 0.001$; $F_2(1, 192) = 0.02$, $p = 0.89$, $\eta_p^2 = 0.000$). A significant interaction occurred between direct association and common associates by subjects ($F_1(1, 62) = 12.42$, $p < 0.001$, $\eta_p^2 = 0.167$; $F_2(1, 192) = 2.22$, $p = 0.138$, $\eta_p^2 = 0.011$): Many common associates produced no significant improvement, unless a strong direct association was present as well ($t(62) = -5.97$, $p < 0.001$). All other interactions remained nonsignificant.

T-tests of all three priming levels against zero reached significance only for *Associative+Semantic* priming at both SOAs, (short: $t(62) = 5.61$, $p < 0.001$; long: $t(62) = 3.53$, $p < 0.01$; see **Table 3**), confirming the interaction from above.

The 2 (type of pure priming: *Associative/Semantic*) × 2 (SOA: 200 ms/1,000 ms) ANOVA yielded significant main effects only in subject analyses for pure priming ($F_1(1, 62) = 4.02$, $p < 0.05$, $\eta_p^2 = 0.061$; $F_2(1, 96) = 0.61$, $p = 0.435$, $\eta_p^2 = 0.006$) and SOA ($F_1(1, 62) = 6.82$, $p < 0.05$, $\eta_p^2 = 0.099$; $F_2(1, 96) = 0.27$, $p = 0.603$, $\eta_p^2 = 0.003$) while the interaction remained nonsignificant.

The 4 (type of priming: *Associative+Semantic/Associative/Semantic*/Sum of *Associative* and *Semantic*) × 2 (SOA: 200 ms/1,000 ms) ANOVA by subjects also showed significant main effects for priming types ($F_1(1, 62) = 18.84$, $p < 0.001$, $\eta_p^2 = 0.485$) and SOA ($F_1(1, 62) = 6.92$, $p < 0.05$, $\eta_p^2 = 0.1$) and no significant interaction.

3.1.4 DISCUSSION

The present study answered McNamara's challenge to address the effects of direct association and semantic relation during visual word recognition in a full factorial fashion (McNamara, 2005, pp. 71, 86). We hypothesized that a direct association can be ubiquitously defined by the statistically significant co-occurrence of two words, whereas semantic similarity can be quantified by the number of common associates.

The ER data revealed a main effect for direct association (strong: 3.62% errors; no: 5.86% errors) as well as for common associates (many: 4.19% errors; no: 5.29% errors). We also found a significant interaction between both factors: Post hoc comparisons showed that error effects of common associations are apparent only if a direct association is likewise present (2.48% errors vs. 5.9% errors for common associates only and 5.8% errors for unrelated word pairs). Because of inconsistent findings across the analyses without any clear interactions with SOA and the relatively low error rates across all participants (rarely >5%), we argue that the error analysis cannot reliably contribute to the question of overadditive versus additive effects of associative and semantic priming.

The RT data of the 2 (direct association: strong/no) × 2 (common associates: many/no) × 2 (SOA: short/long) ANOVA suggest that the direct spread of activation can indeed account for classic associative priming, as it facilitated word recognition more effectively as SOA increased (Hutchison, 2003). Moreover, our proposal to define semantic similarity by the number of common associates resulted in no priming effects at a long SOA. This confirms previous studies and can be interpreted by increased semantic competition (Balota et al., 1992; Lucas, 2000). In summary, even though the relatedness proportion within the stimulus set needs to be manipulated for a definite answer (McNamara, 2005; Neely, 1991), associative priming seems to be more strategic and semantic priming more automatic.

Direct associations that are independent from semantic similarity were called into question by Lucas (2000), Hutchison (2003), and McNamara (2005), but seem to be a theoretical possibility if one relies on co-occurrence statistics. To our knowledge, we provide the first reported true crossover interaction of both types of pure priming with SOA, which cannot be eliminated by a monotonic transformation of the data (Wagenmakers et al., 2012). Hence, the 2 (type of priming: *Associative/Semantic*) × 2 (SOA: 200 ms/1,000 ms) ANOVA revealed that pure *Associative* and *Semantic* priming were equally effective at the short SOA, while *Associative* priming was significantly stronger than *Semantic* priming as SOA increased. In addition, pure *Associative* priming increased significantly as SOA increased (+18 ms), while *Semantic* priming showed only a nonsignificant trend toward decreasing effects at the long SOA (−11 ms). The weaker effect of pure *Semantic* priming might be explained by two opposing mechanisms: On the one hand, there is the facilitatory effect of distinctive semantic features that a prime and target word have in common, thus resulting in pre-activation of the target. On the other hand, the interfering process of semantic competition increases at longer SOAs (Plaut & Booth, 2000).

The interaction of both factors from the 4 (type of priming: *Associative+Semantic/Associative/ Semantic*/ Sum of *Associative* and *Semantic*) x 2 (SOA: 200 ms/1,000 ms) ANOVA also points toward an independent contribution of both pure priming effects: *T*-tests consistently revealed no significant difference between *Associative+Semantic* priming and the sum of *Associative* and *Semantic* priming at both SOAs. Furthermore, the successful dissociation of *Associative* from *Semantic* priming is strongly supported by JZS Bayes factor analysis, as it consistently favored the additive model, even though the effect was relatively weak at the short SOA. Congruent *t*-tests for *Associative+Semantic* and the sum of *Associative* and *Semantic* priming, however, support the assumption of additive pure priming also at the short SOA.

In conclusion, the outlook to no longer rely on human performance for stimulus selection in lexical decision tasks seems very promising: Extracting associative data directly from a corpus saves time, and such an approach can be generalized more easily to any possible word pair. This permits more complex challenges such as creating a full factorial manipulation of direct association and semantic similarity. While the presently most successful co-occurrence-based models in psychology (e.g., Mandera et al., 2017; Mikolov et al., 2013) might be applicable to dissociate associative from semantic priming as well, we propose that the theoretical difficulty of separating these two effects can be resolved by a single principle: The log likelihood that two words co-occur significantly more often in the sentences of a large corpus than predictable by their single word frequencies.

3.1.5 SUPPLEMENTARY MATERIALS

The online version of this article (https://doi.org/10.3758/s13423-018-1453-6) contains supplementary stimulus material, which is available to authorized users.

3.2 STUDY B

Table 4: *Bibliographic information of STUDY B.*

Title	**Functional connectivity of the left inferior frontal gyrus during semantic priming**
Authors and Affiliations	Andre Rölke-Wellmann[a], Markus J. Hofmann[a] [a] General and Biological Psychology, Bergische Universität Wuppertal, Germany
Publication Outlet	Neuroscience Letters
Publication Type	Journal Article
Publication Year	2020
Publication Status	Published
DOI	https://doi.org/10.1016/j.neulet.2020.135236
Abstract	Recent applications of computationally calculated word co-occurrences allowed the prediction of left inferior frontal gyrus (LIFG) activation during semantic word processing. Hence, an interactive activation model, the associative read-out model (AROM), utilizes co-occurrences in its semantic processing layer and proposes connectivity from the LIFG along the ventral visual stream. Direct empirical evidence for its connectivity assumptions is so far missing, however. In this study, we employed psychophysiological interaction analysis on the neuroimaging data of a semantic priming experiment, targeting the LIFG as main region to resolve semantic conflicts. We further manipulated the prime and target word by co-occurrence-based direct association and semantic similarity in a full-factorial design. At a low semantic similarity, we observed increased functional connectivity of the LIFG to the fusiform gyrus, the hippocampus, the anterior cingulate cortex and the orbitofrontal cortex, indicating a connective pattern analogous to the semantic layer of the AROM. Surprisingly, a low (compared to a high) direct association showed no difference in brain activation, which raises the question about the diverging cognitive processes of the two priming types.

3.2.1 INTRODUCTION

Previous research on associative and semantic priming highlighted the left inferior frontal gyrus (LIFG) as critical region for the suppression of irrelevant semantic predictions (Copland et al., 2007; Sachs et al., 2011; Tivarus et al., 2006; Weber et al., 2016). There were, however, inconsistent results: Some studies reported that activation in the LIFG increased for associatively related words (Copland et al., 2007; Sachs et al., 2011), while others observed a decrease of LIFG activation (Tivarus et al., 2006; Weber et al., 2016). Such contradictory findings raise concerns about the generalization of effects as those studies relied on free association norms, in which the priming types of direct association and semantic similarity are usually confounded (McNamara, 2005; STUDY A). Hence, the LIFG could have been activated to resolve semantic conflicts of presumably "purely" associated word pairs in the one study, but was comparably lower activated in the other study with less confounds. Thompson-Schill and Botvinick (2006, p. 402) argued that "investigators would be better served by developing a more explicit framework in which the effects of manipulations such as association strength can be more formally assessed".

Recently, researchers were able to clearly separate associative from semantic priming by using word co-occurrence statistics, which revealed an additive and thus unconfounded contribution of the two priming types (STUDY A). In such an approach, a direct association is computed by the log likelihood that two words co-occur in the same sentence (Hofmann et al., 2011; Quasthoff et al., 2006; Dunning, 1993). The semantic relationship can be defined by the number of common direct associates, which represent shared semantic features (Quasthoff et al., 2006; Rapp, 2002). This allows a full-factorial manipulation: DRIVER and CAR are often used in the same sentence and are semantically related; DEVIL and DETAIL are semantically distant but are frequently used in the idiom *"The DEVIL is in the DETAIL"*; PLATFORM and STAGE occur in similar sentences but do not co-occur in the same sentence significantly often.

On the basis of co-occurrences, Hofmann and Jacobs (2014) made full-Bonferroni-corrected predictions of LIFG activation. Presenting acoustic stimuli, Frank and Willems (2017) found diverging brain activations for co-occurrence-based associative and semantic relations. The fusiform gyrus and the superior temporal gyrus responded to direct associations, while the anterior temporal cortex and parietal regions were more active for semantic similarity. In addition, recent interactive activation models, which utilize co-occurrences such as the associative read-out model (AROM, Hofmann et al., 2011; cf. McClelland & Rumelhart, 1981), propose model-to-brain-data connections for semantic processing. Thus, Hofmann and Jacobs (2014) related the semantic structure of the model to the temporal cortex (retrieval and adaptation of information, Bedny et a., 2008; Binder et al., 2009) and to the LIFG (semantic competition, Bedny et al., 2008; Binder et al., 2009; Carreiras et al., 2014; Weber et al., 2016), while those regions receive orthographic information from lower-level areas like the fusiform gyrus (Binder et al., 2009; Carreiras et al., 2014; Kronbichler et al., 2004; McCandliss et al., 2003; Vinckier et al., 2007).

The aim of the present study was to utilize a full-factorial manipulation of co-occurrence-based direct association and semantic similarity, and to tie the architectural assumptions of the AROM to the functional connectivity in the LIFG. Therefore, our analysis contained psychophysiological interactions (PPI) to set activity in various areas in functional relation to an experimental manipulation (O'Reilly et al., 2012). Potential regions for co-activation with the LIFG included not only the fusiform gyrus as orthographic-semantic interface, but also the anterior cingulate cortex (ACC), which has been discussed to support the detection of semantic conflicts (Bedny et al., 2008; Botvinick et al., 2001; Hofmann et al., 2008a; Weber et al., 2016). Another candidate for a connection with the LIFG was the hippocampus by computing the semantic feature overlap of the prime and target word (Binder et al., 2009; Ranganath & Ritchey, 2012; Yassa & Stark, 2011).

3.2.2 METHOD

The stimuli consisted of 200 noun–noun word pairs, 50 for each priming condition of the 2 (Direct association: Strong / No) x 2 (Semantic similarity: High / No) design, and 200 noun word–nonword pairs. We matched the primes and targets in all priming conditions on word length (3-8 letters), Leipzig frequency class (range: 7-15; Hofmann et al., 2011; Quasthoff et al., 2006) and number of orthographic neighbors (all *F*s < 1; see **Table 2** in STUDY A for more information).

The direct association between two words was calculated based on co-occurrence statistics, using a 43 million sentences corpus with more than 7.5 million word types. For instance, the word COFFEE occurs 17,151 times in the corpus, the word CUP 2,612 times, while both co-occur 1,002 times. Then we used a log likelihood test to determine whether the words co-occur significantly more often together in sentences than expectable by their single-word frequency (Hofmann et al., 2011; Quasthoff et al., 2006; Dunning, 1993). The number of shared direct associates reflected the degree of semantic similarity, as it implies that two words fit well into the same context (Quasthoff et al., 2006; Rapp, 2002). The words MORNING and EVENING, for example, share many direct associates (e.g. THUNDER, DARKNESS, RAIN, FOG, etc.) allowing their replacement in several contexts. The targets with strong direct associations and/or high semantic similarity to the prime were selected to be the top associates. The word–nonword pairs comprised a different set of prime words. They were matched to the primes and targets of the word–word conditions, but without any association to them. Concerning the target nonwords, we replaced two letters from the original target words (consonants and vowels from all positions equally often and in all variations). Half the nonwords followed the phonological rules of German language, while the other half consisted of unpronounceable random letter strings. Moreover, we included 25 null events of fixation crosses only. Twenty unrelated practice trials (word–word and word-nonword pairs evenly distributed) with identical selection criteria as above were prepared for familiarization with the paradigm.

Thirty-two right-handed, native German speakers (20 female, *M* = 26.53 years, *SD* = 5.2 years) participated in the study. One participant had to be excluded from analyses due to brain damage in the temporal lobe during childhood. None of the remaining subjects reported language, psychiatric or neurological disorders. The experiment was conducted in accordance with the Declaration of Helsinki and followed standard MRI guidelines.

Each participant received a unique pseudorandomized order of trials with no more than three word (or nonword) targets in sequence. The stimuli were presented in uppercase and in a black font (Times New Roman) on a white background. A trial started with the presentation of the prime word (150 ms) at the center, followed by a blank screen for 50 ms or 850 ms. Next, the target word was presented for 200 ms and replaced by eight hash characters (########) for 1300 ms, both conforming a response window of 1500 ms in total. Trials were separated by a centered fixation cross for 1,000 to 3,000 ms. Participants were instructed to focus on the fixation cross and to respond as fast and as accurately as possible.

Data acquisition was carried out at the Center for Cognitive Neuroscience Berlin on a Siemens Magnetom 3T TrioTim syngo MR B17 scanner with a 12-channel receiver head coil. Stimuli were presented via a mirror above the head of the participants. To eliminate inhomogeneities, shimming was applied prior to scanning. Functional (T2*) and structural slices (T1) were aligned along the AC/PC line. The echo planar imaging for functional data consisted of 37 slices, recorded in descending order with a TR of 2000 ms, a TE of 30 ms and an in-plane resolution of 3x3 mm (FOV 192 mm, matrix size 64 x 64 mm). The parameters for structural imaging were set to 176 slices in descending order, a TR of 1900 ms, a TE of 2.52 ms and an in-plane resolution of 1 x 1 mm (FOV 256 mm, matrix size 256 x 256 mm).

The imaging data was pre-processed and analyzed using SPM12 (The FIL Methods Group; http://www.fil.ion.ucl.ac.uk/spm/). Slice Timing with a middle reference slice corrected the temporal acquisition differences in functional images. Images were realigned to their mean, co-registered with the structural images, normalized to the Montreal Neurological Institute (MNI) standard with voxel sizes of 2 x 2 x 2 mm, and smoothed with a Gaussian kernel of 8 mm FWHM. On a single subject level, the correctly identified target words of each condition were added to the General Linear Model (GLM) in separate predictors. The subsequent hashtags were submitted separately for each condition to partial out movement effects related to the key pressing response. Separate regressors were included for the null events, the incorrectly identified targets, the nonword targets, the primes and the six realignment parameters from data pre-processing. The high-pass filter was set to 1/128 Hz, using the canonical hemodynamic response function (HRF) and its temporal derivatives as basic functions. The output was estimated using an autoregressive AR(1) model during the Restricted Maximum Likelihood (ReML) method. For each subject, we created four *t*-contrasts to reflect all levels of our experimental conditions. These single subject contrasts were submitted to the design specification on a group level to perform a 2 (Direct association: Strong/No) × 2 (Semantic similarity: High/No) ANOVA. We also conducted a post-hoc analysis including gender as a covariate. This did not change the overall result pattern (see **Appendix A** of STUDY B). The cluster threshold was set to 20 voxels for a Family-Wise Error (FWE)-corrected *p* value of 0.05 to reduce Type I errors. To further examine hypothesis-driven activations along the ventral visual stream, we used an uncorrected *p* value of 0.001 (cluster threshold ≥ 50 voxels).

PPI analysis was performed to investigate functional connectivity of our seed region, the LIFG. For each participant, we first extracted voxels of interest (VOI, spherical shape, radius of 6 mm) of an area in the LIFG that showed a significant activation for the group level main effect. To account for inter-individual differences in functional anatomy, we allowed small variations from the center of each VOI to the cluster peak coordinate of the group level main effect (MNI: -28 / 24 / -2; **Table 5**; O'Reilly et al., 2012). Those variations were limited by ensuring that the VOI was still located in the LIFG activation cluster. The PPI GLM was created for all four experimental conditions separately. Each GLM analysis contained regressors for the interaction term of the VOI signal and the condition as well as the corresponding main effects to partial out effects solely related to either the VOI signal or the condition. Finally, we submitted the resulting subject level *t*-contrasts of the interaction term to a group level 2 × 2 ANOVA. The cluster threshold was set to 20 voxels for an uncorrected *p* value of 0.001. We did not apply any alpha correction, as event-related PPIs bear the risk of many false negatives and are generally of low power (O'Reilly et al., 2012).

3.2.3 RESULTS

In a 2 (Direct association: Strong/No) × 2 (Semantic similarity: High/No) ANOVA of response times, we observed significant effects for direct association ($F(1, 30) = 53.31$, $p < 0.001$, $\eta_p^2 = 0.640$; Strong: 654 ms, No: 696 ms) and semantic similarity ($F(1, 30) = 31.55$, $p < 0.001$, $\eta_p^2 = 0.513$; High: 664 ms, No: 685 ms), and no interaction ($F(1, 30) = 1.44$, $p = 0.239$, $\eta_p^2 = 0.046$).

Concerning the neuroimaging data, we first contrasted the two priming types against the null event condition to confirm their influence on brain activation. A one sample *t*-test of high direct association (including data from High/High and High/No) versus the null events showed changes of neural activation in large clusters covering the bilateral IFG, middle frontal gyrus, inferior parietal cortex and caudate, and in the right superior frontal gyrus and ACC. A high semantic similarity (including data from

High/High and No/High) contrasted against the null events revealed an activation pattern of the bilateral IFG, middle frontal gyrus and superior frontal gyrus, the left ACC and the right inferior parietal cortex.

The 2 × 2 ANOVA revealed significant changes in brain activity for semantic similarity. No shared associates of the prime and target resulted in increased hemodynamic responses in the bilateral IFG (including the insula), the superior frontal gyrus and occipital cortex, the left precentral gyrus, and in the right ACC and midbrain (**Table 5**). Applying an uncorrected $p < 0.001$ further revealed effects such as in the left (but not right) fusiform gyrus ($F(1,240) = 22.58$; peak MNI: -32 / -58 / -14) and middle temporal gyrus ($F(1,240) = 23.08$; peak MNI: -46 / -4 / -18) (**Fig. 7** a) and b)).

No significant differences (including an uncorrected $p < 0.001$) in neural activity were found for direct association or the interaction of priming types.

Table 5: *Significant brain regions for the main effect semantic similarity (FWE corrected p < 0.05; cluster threshold > 20 voxels).*

Region	BA	Hemisphere	Cluster Size in Voxels	MNI Coordinates x	y	z	*F* Value df = 1, 240
Inferior frontal gyrus & Insula	13/47	L	83	-28	24	-2	36.82
	13/45/47	R	135	34	26	2	46.02
Superior frontal gyrus	6/8	L	158	-6	10	48	50.24
	6/8	R	70	10	14	50	43.96
Occipital cortex	18	L	42	-28	-84	-10	34.32
	17/18	R	129	18	-96	0	64.27
Precentral gyrus	6	L	62	-44	4	32	34.10
Anterior cingulate cortex	32	R	22	8	32	28	33.87
Midbrain	-	R	54	2	-12	-6	38.02

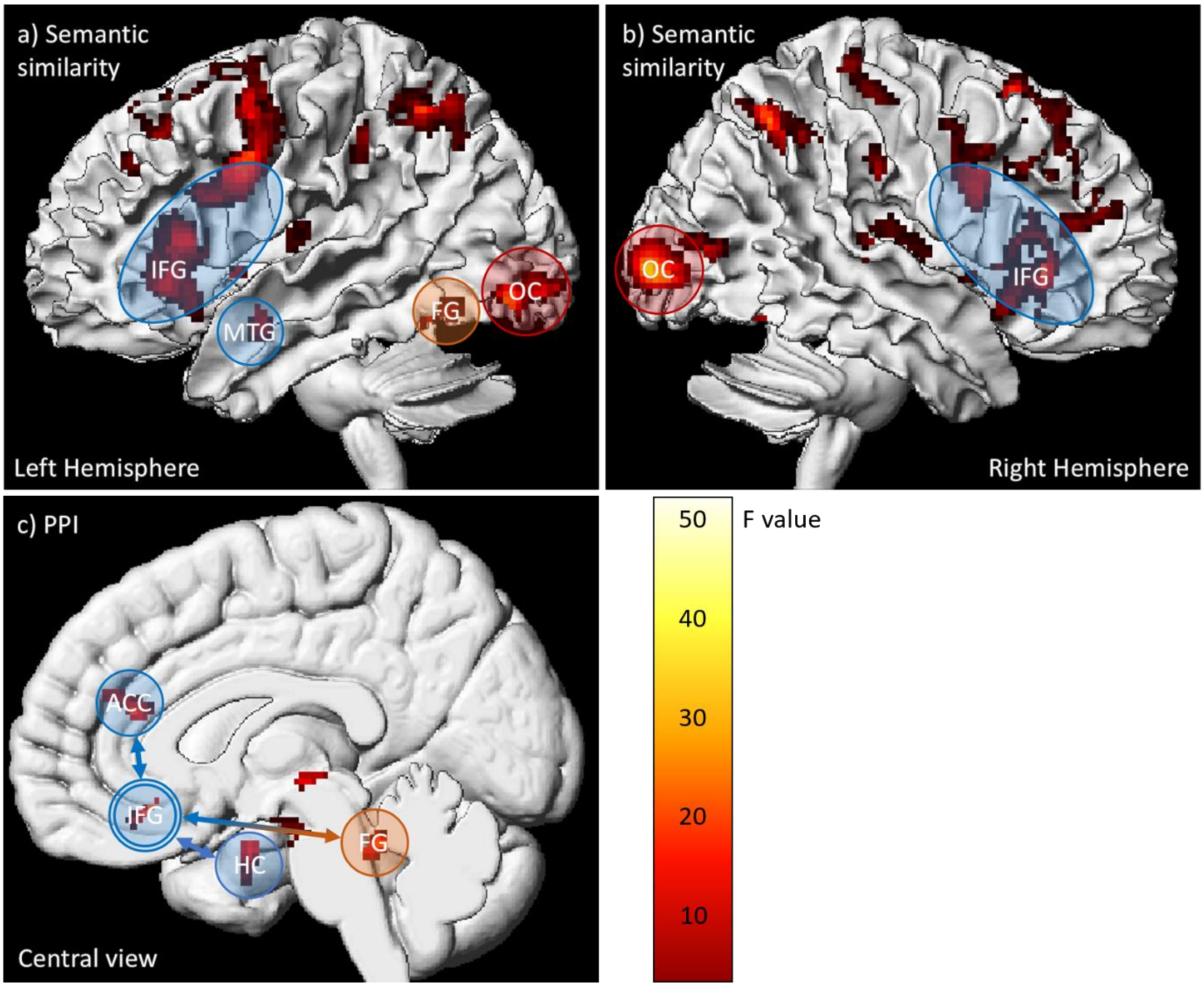

Fig. 7 – *a) & b): Significant brain regions for semantic similarity at an uncorrected p < 0.001. c) Co-activations to the left inferior frontal gyrus for semantic similarity based on the PPI analysis. The colorization indicates the proposed functional assignment in an interactive activation model of word recognition (e.g. Carreiras et al., 2014; Hofmann & Jacobs, 2014): Red = Visual features, Orange = Orthographic word forms, Blue = Semantics. Highlighted regions: ACC = Anterior cingulate gyrus, FG = Fusiform gyrus, HC = Hippocampus, IFG = Inferior frontal gyrus, MTG = Middle temporal gyrus, OC = Occipital cortex. Visualization done via xjView toolbox (http://www.alivelearn.net/xjview).*

PPI analysis of the semantic similarity main effect with the LIFG (MNI: -28 / 24 / -2; **Table 5**) as seed region revealed a significant functional connectivity to the bilateral IFG (including the insula), the left cerebellum, anterior fusiform gyrus and parahippocampus, the left-to-central midbrain, and the right hippocampus, orbitofrontal cortex and ACC (**Table 6** and **Fig. 7** c)).

Table 6: *Significant psychophysiological interactions with the left inferior frontal gyrus as seed region for the main effect of semantic similarity (uncorrected p < 0.001; cluster threshold > 20 voxels).*

Region	BA	Hemisphere	Cluster Size in Voxels	MNI Coordinates x	y	z	*F* Value df = 1, 240
Inferior frontal gyrus & Insula	13/47	L	45	-42	8	-7	18.25
	47	R	34	40	20	-11	17.77
Cerebellum & Fusiform gyrus & Parahippocampus	36	L	372	-13	-38	-25	22.73
Hippocampus	-	R	47	25	-2	-26	20.87
Orbitofrontal cortex	11	R	32	5	31	-15	18.90
Anterior cingulate cortex	32	R	74	9	33	17	17.03
Midbrain	-	L	65	-4	-14	-21	16.55
	-	Central	42	0	-18	-5	12.95

3.2.4 DISCUSSION

We investigated the functional connectivity of the LIFG in a co-occurrence based semantic priming study to provide direct empirical evidence for the implementation of the semantic processing layer in the AROM (Hofmann et al., 2011; Hofmann et al., 2014). We found an increased connectivity of the LIFG to the left fusiform gyrus and cerebellum, the right IFG, orbitofrontal cortex, ACC and to the hippocampus if the semantic similarity of prime and target was low. In addition, a low semantic similarity activated the bilateral superior frontal gyrus, occipital cortex and the left precentral gyrus without any functional dependence on the LIFG. The direct association of two words did not affect brain activity. Furthermore, the neuroimaging data did not show any interaction of the two priming types.

Semantic competition is implemented in the AROM by calculating the most likely word unit among all associates pre-activated by a prime. If the prime and target word share a high number of associates, the AROM predicts facilitated target recognition (= lower demand on the LIFG). On the other hand, a low amount of feature overlap, and thus many pre-activations that compete with the target, delays the identification of the target (Hofmann et al., 2014). This requires the LIFG to suppress conflicting associations as indicated by our main effect of semantic similarity (Sachs et al., 2011; Weber et al., 2016).

Recent research suggested that higher-level regions provide top-down feedback to the fusiform gyrus during the selection of visual word forms (Carreiras et al., 2014; Kringelbach, 2005; Price & Devlin, 2011; Ranganath & Ritchey, 2012; Weber et al., 2016). In the light of the observed interactivity between the left IFG and the left fusiform gyrus, it appears that areas of orthographic processing and the semantic network enable a two-way evaluation of a word, analogous to the layered structure of the AROM (cf. Fig. 6 in Hofmann et al., 2014). Contrary to the predictions by Hofmann and Jacobs

(2014) however, PPI analysis indicates a direct connection of the fusiform gyrus and the LIFG by skipping the (anterior) inferior and middle temporal cortex. While fMRI is considered to be rather insensitive to temporal effects (Sachs et al., 2011; Tivarus et al., 2006), the findings by Bedny et al. (2008) also suggest that the temporal cortex is more involved into explicit semantic retrieval and less into the suppression of conflicting co-activations. This supports our observation of slightly increased responses in the middle temporal gyrus at a low semantic similarity for an uncorrected $p < 0.001$, only. As our analyses were hypothesis-driven, we would therefore consider the contribution of the temporal cortex during (implicit) semantic priming tasks to be comparably weaker but still relevant for a successful recognition of the target word.

PPI analysis further revealed a functional connectivity of the LIFG to the ACC and the cerebellum, which have been proposed to detect semantic conflicts (Bedny et al., 2008; Botvinick et al., 2001; Hofmann et al., 2008a). Reciprocal co-activation of the ACC and the orbitofrontal cortex was also discussed by Kringelbach (2005) during decision making. Taken together, this could explain the current findings of a functional dependency of those regions to the LIFG, e.g. by supporting the identification of the target word among other pre-activated words by the prime.

Finally, our PPI results hint towards a functional connectivity between the LIFG and the hippocampus. The hippocampus is usually associated with the integration of new semantic knowledge as well as object familiarity and recollection (Ranganath & Ritchey, 2012; Yassa & Stark, 2011). As pointed out by Ranganath and Ritchey (2012), familiarity-based recognition includes the processing of semantic relations of words (Binder et al., 2009). This information could have been supplied from the hippocampus to the LIFG to initiate a suppression of dispensable co-activated words, for example. Importantly, activation in the hippocampus was revealed solely in the PPI analysis, thus highly dependent on the LIFG. This suggests a strong coupling of those two regions which emerges for demanding cognitive tasks such as deep mental searches for semantic relations. The involvement of the hippocampus not only during the encoding of new memory but also during word recognition further implies that connectionist models like the AROM should benefit from an implementation of the hippocampal system also for the simulation of semantic priming tasks (Kumaran & McClelland, 2012).

The occipital cortex elicited increased neural responses for word pairs of low semantic similarity without any dependency on LIFG activation. Interactive models of visual word recognition assume that the occipital cortex is not in direct functional connection with the IFG but interconnected via the fusiform gyrus for integration, which is probably reflected by our results (Carreiras et al., 2014; Hofmann & Jacobs, 2014). It is possible that the increased response of the occipital cortex for a target of low semantic overlap to the prime was mediated by top-down influences (Hofmann et al., 2014).

While directly associated word pairs generally activated regions responsible for word recognition, we could not observe any significant differences in brain activity for a high versus no direct association. This is even more surprising as behavioral data revealed a strong priming effect of 42 ms. First, we cannot exclude the possibility of undetected effects based on the employed MRI technology, especially in the temporal cortex (Sachs et al., 2011; Tivarus et al., 2006). Furthermore, McNamara (2005) and Sachs et al. (2011) argued that the evaluation of a semantic similarity requires a conscious and much deeper mental search than a direct association, which might explain the current neuroimaging data. Many pre-activated semantic features of the prime had to be matched to the target word independently on their relevance for the target. This could have potentiated ventral visual stream activation in the case of the semantic similarity manipulation. On the other hand, a direct association – unconfounded by semantic similarity due to the co-occurrences method – could have been processed rather fast and without that much effort on the IFG-system.

The dissociability of the two priming types was on debate for a long time but suggested by STUDY A if using computationally calculated word co-occurrences instead of relying on free association norms, for example. Their independent processing is also supported by the current study as no interactive effects were revealed. In sum, our observations imply that co-occurrences allow a “clean” experimental manipulation of word-word relations and also entail model-to-brain-data connections. Hence, future studies may want to use such computationally calculated word co-occurrences to directly link neuroimaging data to their model.

3.2.5 APPENDIX A – GENDER AS POST-HOC COVARIATE

In a post-hoc analysis, we added gender as covariate (coded as binaries in SPM12). The resulting activation pattern was similar for an uncorrected $p < 0.001$ and FWE corrected $p < 0.05$. Identically to the analysis without gender as covariate, a main effect for semantic similarity showed differences in the neural response of the bilateral IFG (including the insula), the superior frontal gyrus and occipital cortex, the left precentral gyrus, and in the right ACC and midbrain (**Table 7**, **Fig. 8**). Applying an uncorrected $p < 0.001$ further revealed effects such as in the left (but not right) fusiform gyrus ($F(1,240) = 16.89$; peak MNI: -30 / -58 / -14) and middle temporal gyrus ($F(1,240) = 16.25$; peak MNI: -48 / -4 / -18).

No significant differences (including an uncorrected $p < 0.001$) in brain activation were found for direct association or the interaction of priming types.

Table 7: *Significant brain regions for the main effect semantic similarity with gender as covariate (FWE corrected $p < 0.05$; cluster threshold > 20 voxels).*

Region	BA	Hemisphere	Cluster Size in Voxels	MNI Coordinates x	y	z	*F* Value df = 1, 240
Inferior frontal gyrus & Insula	13/47	L	29	-30	24	-4	32.46
	13/45/47	R	90	32	24	-6	39.56
Superior frontal gyrus & Anterior cingulate cortex	6/8/32	L	103	-6	10	48	42.87
	6/8/32	R	50	10	14	50	37.93
Occipital cortex	18	L	20	-14	-90	-2	33.86
	17/18	R	94	18	-96	0	52.91
Midbrain	-	R	29	2	-12	-4	33.39

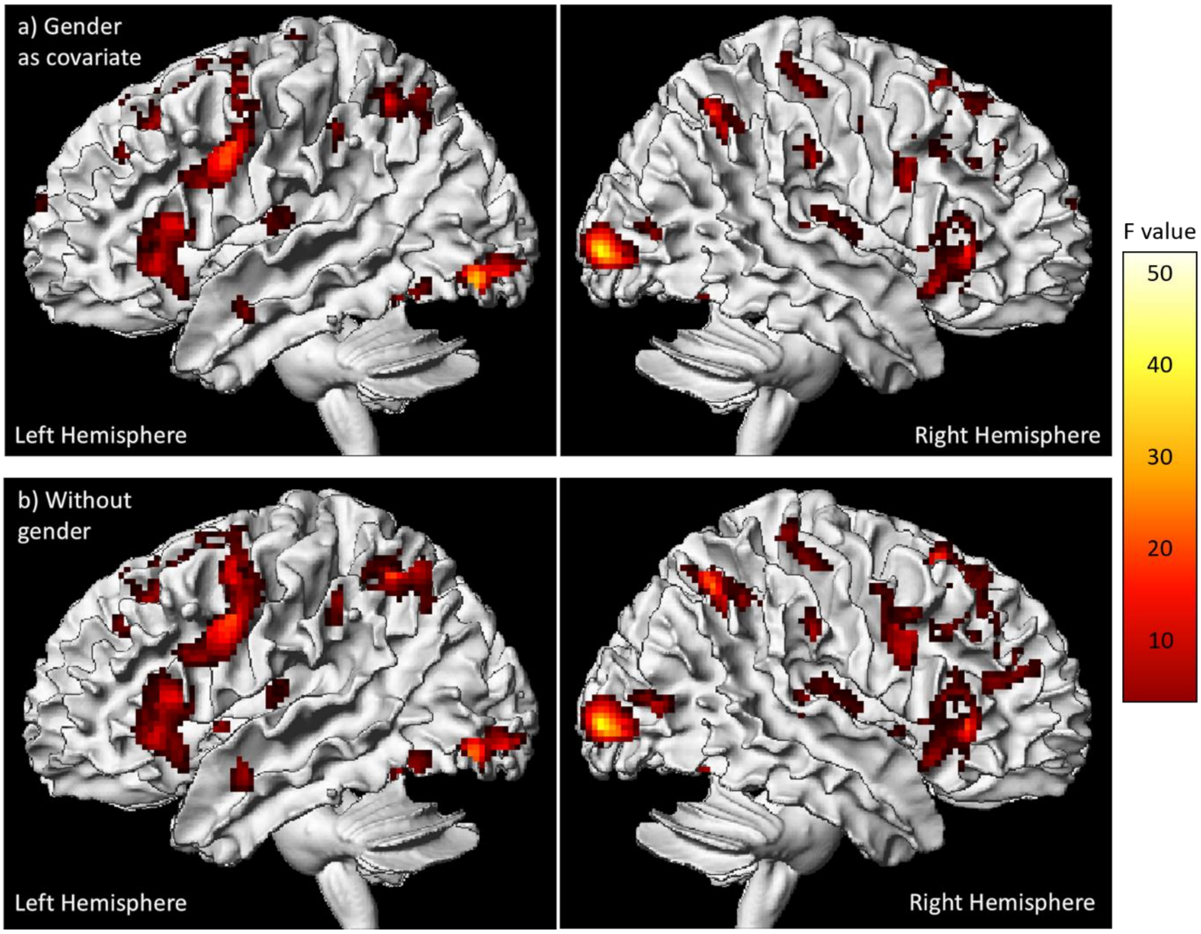

Fig. 8: *Significant brain regions for semantic similarity at an uncorrected $p < 0.001$ by a) using gender as covariate and b) not using gender as covariate.*

3.3 STUDY C

Table 8: *Bibliographic information of STUDY C.*

Title	**Fixation-related NIRS indexes retinotopic occipital processing of parafoveal preview during natural reading**
Authors and Affiliations	Andre Rölke-Wellmann[a], Christian Vorstius[a], Ralph Radach[a], Markus J. Hofmann[a] [a] General and Biological Psychology, University of Wuppertal, Germany
Publication Outlet	NeuroImage
Publication Type	Journal Article
Publication Year	2020
Publication Status	Published
DOI	https://doi.org/10.1016/j.neuroimage.2020.116823
Abstract	While word frequency and predictability effects have been examined extensively, any evidence on interactive effects as well as parafoveal influences during whole sentence reading remains inconsistent and elusive. Novel neuroimaging methods utilize eye movement data to account for the hemodynamic responses of very short events such as fixations during natural reading. In this study, we used the rapid sampling frequency of near-infrared spectroscopy (NIRS) to investigate neural responses in the occipital and orbitofrontal cortex to word frequency and predictability. We observed increased activation in the right ventral occipital cortex when the fixated word N was of low frequency, which we attribute to an enhanced cost during saccade planning. Importantly, unpredictable (in contrast to predictable) low frequency words increased the activity in the left dorsal occipital cortex at the fixation of the preceding word N-1, presumably due to an upcoming breach of top-down modulated expectation. Opposite to studies that utilized a serial presentation of words (e.g. Hofmann et al., 2014), we did not find such an interaction in the orbitofrontal cortex, implying that top-down timing of cognitive subprocesses is not required during natural reading. We discuss the implications of an interactive parafoveal-on-foveal effect for current models of eye movements.

3.3.1 INTRODUCTION

To explore the neural effects of word frequency and predictability during visual word recognition, some neuroimaging studies imitated the reading process by presenting sentences word-by-word for 200–300 ms to match the average duration of one fixation (e.g. Buchweitz et al., 2009; Dambacher et al., 2009; Hofmann et al., 2014; Rayner, 1998; Yarkoni et al., 2008). Utilizing functional near-infrared spectroscopy (fNIRS) in such a setting, Hofmann et al. (2014) reported increased activity in the occipital cortex for low predictability words as a result of false top-down predictions. Moreover, the medial orbitofrontal cortex (OFC) responded to unpredictable low frequency words, only, suggesting an OFC-driven switch between bottom-up or top-down mode to evaluate the validity of a prediction (Bar et al., 2006; Nobre et al., 1999). Whole sentence reading, however, can increase the amount of bottom-up information (independently of lexical variables), reducing the demand of the OFC as "timer" because prediction errors are less likely to occur (Hofmann et al., 2014; Kiebel et al., 2008; Murray et al., 2014; Roesch & Olson, 2005). Hence, the occipital cortex with its hierarchical and retinotopic organization might guide saccade planning during free visual exploration tasks (Larsson & Heeger, 2006; Mazer & Gallant, 2003; Merriam et al., 2007; Nakamura & Colby, 2000; Saber et al., 2015). More specifically, the extrastriate regions (V2, V3, V4, etc.) may pass relevant information for saccade preparation to the dorsal (via V2 to V3) and the ventral stream (via V2 to V4; Saber et al., 2015).

As the absence of parafoveal influences or regressive eye movements at a serial presentation of words form a rather artificial take on reading (Himmelstoss et al., 2019; Kretzschmar et al., 2015), fixation-related neuroimaging grew in popularity to observe hemodynamic responses in an ecologically more valid setting of natural reading (Hutzler et al., 2007). Methodologically, every fixation on a word can be used as marker of an event, assuming that each evoke a specific neural response (e.g. Dimigen et al., 2011; Hutzler et al., 2007; Marsman et al., 2012; Richlan et al., 2014; Schuster et al., 2016). Using fixation-related fMRI in a sentence reading paradigm, Schuster et al. (2016) observed frequency and predictability effects in areas commonly associated with visual word recognition such as the inferior frontal gyrus, middle temporal gyrus and the occipito-temporal area. However, one fixation on a word includes multiple processing steps such as the initial familiarity check, lexical access, saccade planning / execution and parafoveal preview, all within a duration of approximately 250 ms (Rayner, 1998, p. 375; Reichle et al., 2003, 2009; Schotter et al., 2014). This raises the question if some of those processing parts might elicit a distinct pattern of activation, which could not be accounted for at a sampling rate of 0.5 Hz (= 2 s). While the temporal resolution of fixation-related fMRI can be increased to exceed an average fixation duration, we also wanted to remain close to Hofmann et al. (2014) in order to investigate their proposal of an engagement of the occipital cortex instead of the OFC during natural reading. Therefore, the current study introduces fixation-related functional near-infrared spectroscopy (fNIRS), which provides a sampling rate of more than 10 Hz to disentangle fixation events.

Moreover, fixation-related fNIRS includes not only the examination of deoxygenated hemoglobin [deoxy-HB], like fMRI (but cf. Huppert et al., 2007), but also allows to investigate the fine-grained coupling of [deoxy-Hb] to oxygenated hemoglobin [oxy-HB], thus enabling their cross-validation (Buxton et al., 2004; Hoshi et al., 2001). The usefulness of such an approach is further established as fNIRS-based language studies reported reliable effects in regions of the word recognition pathway (e.g. in the occipital and temporal cortex, the inferior frontal gyrus, and the OFC), even though only the top 15 mm of the cortex are captured (Gervain et al., 2011; Hofmann et al., 2014; Horovitz & Gore, 2004; Quaresima et al., 2012). The spatial resolution, however, is rather coarse to relate effects to smaller subregions (Zeff et al., 2007).

During natural reading, eye movements consistently reveal shorter fixations for high frequency and high predictability words (Inhoff & Rayner, 1986; Reichle et al., 2003, 2009). While both effects can emerge at very early stages of lexical processing (~140 ms after stimulus presentation; e.g. Himmelstoss et al., 2019; Sheridan & Reingold, 2012), most studies indicate their independence (e.g. Rayner et al., 2004) with some evidence pointing towards interactive effects (Hand et al., 2010; Sereno et al., 2018; but see Slattery et al., 2012). Hand et al. (2010) suggested that the distance from the pre-target fixation to the target word beginning (launch distance) might be a determining factor to those ambiguous findings, as parafoveal information might be more accessible at a close distance. They found significant interactions only at short launch distances (predictability effect for low frequency words) and medium launch distances (predictability effect for high frequency words) but not at long distances. Slattery et al. (2012), on the other hand, criticized that launch distance can hardly be under experimental control, as it requires a post-hoc split of the analyzable data. Accordingly, lexical influences from the next word on the currently fixated word (= parafoveal-on-foveal effect; PoF) also prove elusive among the existing literature as some failed to find such effects (e.g. Angele et al., 2015; Degno et al., 2019; Drieghe, 2011; Fitzsimmons & Drieghe, 2013; Kretzschmar et al., 2015; Schotter et al., 2012), while others favor their existence (e.g. Hand et al., 2010; Kliegl et al., 2006; Radach et al., 2013; Risse & Kliegl, 2014; Snell & Grainger, 2019). When coregistering electroencephalography (EEG) signals with eye movements during natural reading, neither Degno et al. (2019) nor Kretzschmar et al. (2015) found behavioral or neural evidence for PoF effects. Other studies, in contrast, observed predictability effects already on pre-target fixations (Hand et al., 2010; Hawelka et al., 2015; Kliegl et al., 2006; Snell et al., 2018), with some of them indicating that predictability might impact word processing even earlier than frequency (Engbert et al., 2005; Hand et al., 2010). Moreover, Schuster et al. (2016) reported increased occipital activation prior to a skipped word, indicating that some information from the following word was processed during the pre-target fixation. In line with the possibility of delayed parafoveal frequency effects, which emerge as late as at the following fixation (Risse & Kliegl, 2014), Snell and Grainger (2019) pointed out the difficulty of resolving the debate on additive / serial or interactive / parallel processing of lexical properties via eye movements, as some effects are often concealed until manipulated in a specific way. Consequently, they encouraged researchers to employ methodological advances as introduced here via fixation-related fNIRS, to test whether or not PoF effects are eliciting distinct neural activation.

We investigated changes of hemodynamic responses during natural reading by utilizing the first fixation on words as events on fNIRS data. We examined frequency and predictability effects on the word itself (N), as well as their influence on the preceding word (N-1). Therefore, we manipulated a target word within a test sentence to be of either high or low frequency, while its predictability was determined by a preceding context sentence (cf. Hofmann et al., 2014). We expected that low frequency and low predictability words resulted in longer fixation durations and increased neural activity in our main target region, the occipital cortex (Hofmann et al., 2014; Inhoff and Rayner, 1986; Schuster et al., 2016). We were interested in the extrastriate region mostly, as it is considered to be increasingly involved into saccade planning and higher order processing (Merriam et al., 2007; Nakamura & Colby, 2000; Saber et al., 2015). Considering that the left part of a word (for left-to-right reading) contains the most valuable information for a successful recognition, we expected a mean landing position slightly left from the center as well as changes of occipital activity to be more accentuated in the right hemisphere (Pisella et al., 2011; Vitu et al., 2001). We also investigated whether the OFC is mandatory for timing of cognitive sub-processes during natural reading (Kiebel et al., 2008; Murray et al., 2014; Roesch & Olson, 2005) or whether saccade planning guided by occipital information is sufficient. At the fixation of N-1, we were interested if parafoveal lexical information of N from the right visual field would modulate eye movements and brain activity, specifically in the left occipital cortex as retinotopic projection.

3.3.2 METHOD

Thirty-six right-handed, native German speakers (27 female, *M* = 23.42 years, *SD* = 3.7 years) with normal or corrected-to-normal vision participated in the study. None of them reported language, psychiatric or neurological disorders. The experiment was conducted in accordance with the Declaration of Helsinki. Participants gave written consent and were compensated for their participation in course credits or cash.

Identical to Hofmann et al. (2014), we used the stimuli from the Potsdam Sentence Corpus, which comprised 144 German sentence units (Dambacher et al., 2009, 2012). Each unit consisted of two context sentences with 3–18 words (*M* = 11.48, *SD* = 2.81), and a test sentence with 9–12 words (*M* = 10.47, *SD* = 0.82). The target word of each test sentence was manipulated to be of either low or high frequency / predictability (full-factorial) with matched length (3–8 letters) and position (6th-8th in sentence) across all conditions (**Table 9**), and was succeeded by at least two more words. High frequency targets occurred more than 100 times per million words, while a low frequency was defined by less than 10 occurrences per million words (Geyken, 2007). Predictability was rated by 151 volunteers in an independent cloze task (Dambacher et al., 2009). High predictability targets exceeded a cloze value of >0.5 (*M* = 0.8, *SD* = 0.13). A cloze value between 0 and 0.1 was set for words of low predictability (*M* = 0.01, *SD* = 0.02).

Table 9: *Descriptive statistics of the manipulated target words. Standard deviations are provided in parentheses.*

	High frequency		**Low frequency**	
Controlled variables	**High predictability**	**Low predictability**	**High predictability**	**Low predictability**
Word form frequency	155.58 (194.63)	155.58 (194.63)	3.76 (2.08)	3.76 (2.08)
Lemma frequency	362.19 (875.30)	362.19 (875.30)	4.87 (2.68)	4.87 (2.68)
Predictability	0.84 (0.13)	0.01 (0.02)	0.83 (0.13)	0.01 (0.02)
Length	5.36 (1.16)	5.36 (1.16)	5.32 (1.11)	5.32 (1.11)
Word position	6.94 (0.76)	6.94 (0.76)	6.94 (0.76)	6.94 (0.76)

The two context sentences of each unit were matched in letter and word count by design. Depending on the predictability of the target, one of them preceded the test sentence. For example, the context sentences of one trial could either be “*Today, the kids had to draw geometrical figures in school*” or “*Today, the kids had to draw domestic insects in school*”. In the test sentence “*At first, the pupils drew a thick circle with their pencil*”, the high frequency word CIRCLE was exchanged by the low frequency word BUG to be in or out of context with either one of the preceding sentences (**Fig. 9**; also see e.g. Fig. 1 in Hofmann et al., 2014, for a depiction of the Latin square design). While all four combinations of high and low frequency / predictability targets were distributed across all stimulus sets, each participant saw only one version per unit and 36 units in total for each condition in a pseudorandomized order (less than four trials from the same condition in a row).

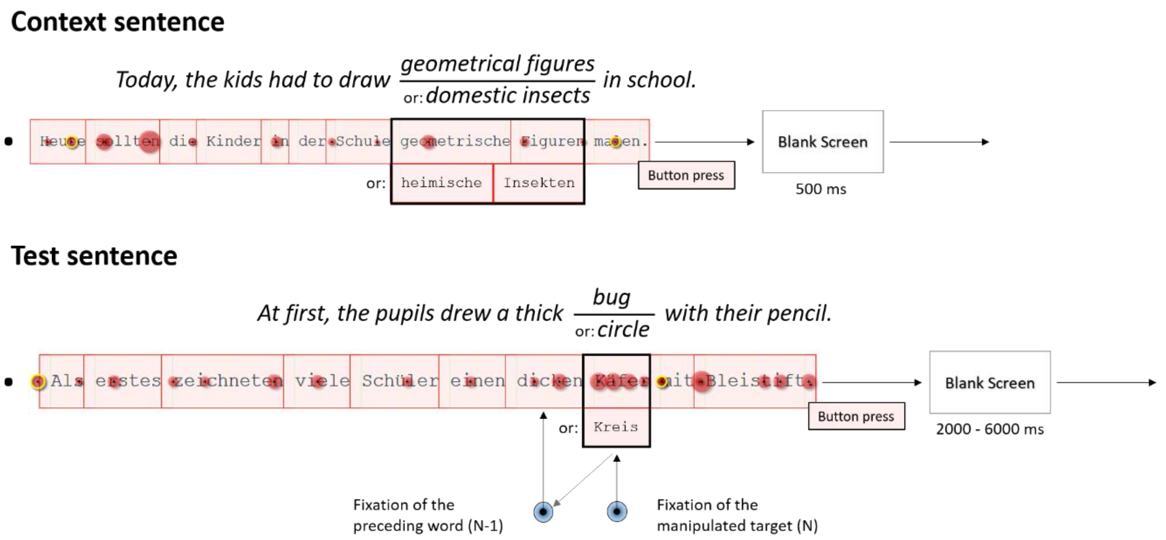

Fig. 9: *Design of one trial in which a context sentence was presented first, followed by a test sentence. The red dots illustrate the fixations of one participant along the sentences, while longer fixations induce larger dots. The low frequency target word BUG in the test sentence is of low predictability if the kids had to draw "geometrical figures" but of high predictability if they had to draw "domestic insects", vice versa for the high frequency target CIRCLE. The analyses focused on the first fixation duration on the target (N) as well as on its preceding word (N-1).*

Stabilized by a chin support, the participants were seated 70 cm away from a 24" monitor. Movements from the right eye were recorded by an EyeLink 1000 Plus system (SR Research) at a sampling rate of 2 kHz. Simultaneously, changes of cerebral (de-)oxygenation were recorded by a NIRScout (NIRx) device at a sampling rate of 10.42 Hz. To capture the absorption spectra of [deoxy-Hb] and [oxy-Hb], the continuous wavelengths were set to 760 and 850 nm respectively. We used a 10-5 system cap with equidistant (3 cm) optode holders. Three sources and three detectors were attached above the nasion, resulting in seven channels to cover the OFC. Another set of three sources and nine detectors (forming 13 channels) recorded brain activity in the occipital cortex, focusing mostly on V2 and V3 (**Table 10**), while the interpolated activation map (see data analysis below) allowed a tentative analysis also in V1.

The experiment consisted of eight practice trials, as well as three blocks of 48 experimental trials each, separated by short breaks. At the beginning of each block, a three-point horizontal calibration was performed. Each trial started with a drift correction dot slightly left from where a sentence would appear. The context sentence was presented in a single line (font: Courier New, size: 18, visual angle < 0.33°) until the participants pressed the 'space' bar. Followed by a short blank screen of 500 ms and another drift correction, a single line test sentence was shown, which contained the manipulated target word. After pressing 'space', a blank screen was presented, jittered between 2000 and 6000 ms. Randomly distributed between one third of all trials, multiple- choice comprehension questions with three possible answers were displayed, to which participants responded by pressing one of the buttons '1', '2' or '3'. After each question, a recalibration procedure was initiated, followed by the next trial.

On average, the multiple-choice comprehension questions were answered with an accuracy of 95.93% (*SD* = 2.97%).

Table 10: *List of channels in the orbitofrontal and occipital cortex, including their projected MNI coordinates and the percentage of the involved subregions (Tsuzuki et al., 2007; Ye et al., 2008). "Optodes (S-D)" contains the respective source and detector of each channel (based on the 10-5 system). For an overview of the channel locations on the cortex, see* **Fig. 10**.

Channels	Optodes (S – D)	Channel-MNI	BA	Area	Percentage
Orbitofrontal					
Ch1	Fp1 – Fpz	-9 / 73 / -6	10	Left frontopolar	0.61
			11	Left orbitofrontal	0.39
Ch2	Fp1 – AF3	-26 / 68 / 4	10	Left frontopolar	1
Ch3	Fp2 – Fpz	15 / 73 / -5	10	Right frontopolar	0.69
			11	Right orbitofrontal	0.31
Ch4	Fp2 – AF4	29 / 69 / 4	10	Right frontopolar	1
Ch5	AFz – Fpz	2 / 68 / 12	10	Medial frontopolar	1
Ch6	AFz – AF3	-12 / 69 / 22	10	Left frontopolar	1
Ch7	AFz – AF4	17 / 69 / 23	10	Right frontopolar	1
Occipital					
Ch8	POz – PO3	-17 / -92 / 40	19	Left V3	0.96
Ch9	POz – PO4	13 / -91 / 40	19	Right V3	0.97
Ch10	POz – Oz	-1 / -96 / 27	18	Medial V2	0.19
			19	Medial V3	0.81
Ch11	O1 – PO3	-28 / -97 / 22	18	Left V2	0.12
			19	Left V3	0.88
Ch12	O1 – PO7	-35 / -98 / 5	18	Left V2	0.77
			19	Left V3	0.23
Ch13	O1 – Oz	-14 / -107 / 11	18	Left V2	0.95
			19	Left V3	0.05
Ch14	O1 – POO9h	-30 / -102 / -1	18	Left V2	1
Ch15	O1 – OI1h	-20 / -107 / 2	18	Left V2	0.99
			19	Left V3	0.01
Ch16	O2 – PO4	27 / -98 / 22	18	Right V2	0.21
			19	Right V3	0.79
Ch17	O2 – Oz	10 / -105 / 10	18	Right V2	1
Ch18	O2 – PO8	35 / -98 / 5	18	Right V2	0.72
			19	Right V3	0.28
Ch19	O2 – OI2h	29 / -102 / -2	18	Right V2	1
Ch20	O2 – POO10h	-22 / 68 / -6	18	Right V2	1

To investigate frequency and predictability effects on eye movements and brain activity, we analyzed the first fixation on every word.[4] We extracted individual first fixation durations only if both, the manipulated target (N) and N-1, were fixated in a sentence to guarantee their deliberate processing. In 34% of all cases either N or N-1 was skipped (both equally often). Moreover, we made sure that the first fixation of N-1 occurred before N. Fixations that included a blink, as well as fixations shorter than 70 ms and more than two times away from the individual condition's mean were excluded from further analyses (5.6% of data). Overall, 61% of data entered the analysis. None of the subjects were excluded due to performance in the multiple-choice task (all >85% correct).

We used the MATLAB and SPM8 based software package NIRS-SPM (Ye et al., 2008) for fixation-related fNIRS data preprocessing and analysis. To account for the age-related changes of light scattering on gray and white matter, an age-dependent differential path length factor was applied (Herold et al., 2017). Temporal preprocessing included a band-pass filter with cut-off frequencies at 0.01 and 0.5 Hz to remove physiological noise and Wavelet-MDL detrending as high-pass motion artifact filter (Herold et al., 2017; Ye et al., 2008). The applied band-pass filter did not account for a potential contamination of [oxy-Hb] effects due to respiration or changes of blood pressure, emerging at approximately 0.1 Hz (Kirilina et al., 2013). A more conservative band-pass filter also influenced [deoxy-Hb] slightly – which is usually less affected by physiological noises for tasks with reliable hemodynamic responses (Klein & Kranczioch, 2019) – suggesting that some part of true event data would have been cut off as well. To overcome this issue, we restricted our findings to coupled effects of [oxy-Hb] and [deoxy-Hb], only. Fixation-related changes in the OFC and occipital cortex were analyzed in separate two-staged general linear models (GLM) for [oxy-HB] and [deoxy-HB]. On the subject-level, channels from the OFC and occipital area (see **Table 10**) were interpolated using inhomogeneous interpolation kernel, which resulted in a full 2D statistical parametric map of both regions (Ye et al., 2008). The first fixation durations were used to model the length of the fixation events, thus effectively partialling out hemodynamic effects explainable by event duration (e.g. the varying BOLD signal undershoots or the overprediction of event amplitudes; Buxton et al., 2004) or task difficulty (Hofmann et al., 2008b). N-1 and N were analyzed in separate GLMs, each including a total of seven predictors. For each experimental condition (Frequency of N High/Low × Predictability of N High/Low), one predictor was submitted consisting of either the first fixation onset of N-1 or N (= four predictors). Only first fixations, which survived the eye movement exclusion criteria (66% of data), were added to those four predictors. Another predictor included all additional (re-)fixations on N-1 or N past the first fixation to account for a potentially incomplete processing. In addition, we added one predictor for the first

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[4] First fixation duration analyses yielded an identical result pattern as single fixation duration (words that were fixated only once), gaze duration (sum of all fixations until leaving a word) and total viewing duration (sum of all fixations, including re-fixations, Radach & Kennedy, 2013). For reasons of redundancy and for better comparison with similar studies, we report first fixation durations, only.

fixation on all other words of the context and the test sentences (also comprising the excluded eye movement data), and a predictor for all inter-trial-blanks. Moreover, we submitted the temporal derivative of the hemodynamic response function to the model. In the second-level analysis, the group beta values were estimated from the individual interpolated betas, and 2 (Frequency of N: High/Low) × 2 (Predictability of N: High/Low) ANOVAs were run for N-1 and N in the OFC and occipital cortex. *F*-contrasts were created for every main effect and interaction. Significant interactions were further analyzed via *t*-tests. We considered effects if [oxy-Hb] and [deoxy- HB] were both below $p < 0.01$. Moreover, we adjusted the alpha value by utilizing partial Bonferroni correction (Sankoh et al., 1997) on the [oxy-HB] ($p < 0.0046$) as well as [deoxy-Hb] related activations ($p < 0.0041$).

3.3.3 RESULTS

3.3.3.1 EYE TRACKING DATA

Descriptive statistics revealed that the mean landing position on N was 2.44 (*SD* = 1.75) and 2.31 (*SD* = 1.9) for N-1, thus slightly left from the mean word length of N (5.44; *SD* = 1.08) and N-1 (5.41; *SD* = 2.9).

We first conducted a 2 (Frequency of N: High/Low) × 2 (Predictability of N: High/Low) ANOVA with first fixation duration of N as dependent variable. We found a significant main effect of frequency ($F(1,35) = 40.5$, $p < 0.001$, $\eta_p^2 = 0.536$; High: 199 ms, Low: 211 ms) and predictability ($F(1,35) = 25.46$, $p < 0.001$, $\eta_p^2 = 0.421$; High: 201 ms, Low: 210 ms), and no significant interaction ($F(1,35) = 0.42$, $p = 0.520$, $\eta_p^2 = 0.012$; **Table 11**).

Next, we submitted the first fixation duration of N-1 to a 2 (Frequency of N High/Low) × 2 (Predictability of N High/Low) ANOVA, which showed a significant main effect for the predictability of N ($F(1,35) = 16.38$, $p < 0.001$, $\eta_p^2 = 0.319$; High: 207 ms, Low: 213 ms) and no effect of frequency ($F(1,35) = 0.39$, $p = 0.538$, $\eta_p^2 = 0.011$; High: 210 ms, Low: 211 ms) or interaction ($F(1,35) = 1.66$, $p = 0.206$, $\eta_p^2 = 0.045$; **Table 11**).

Table 11: *Mean first fixation duration (in ms) of the experimental conditions. Standard errors are provided in parentheses.*

	High frequency N		**Low frequency N**	
Fixation	**High pred. N**	**Low pred. N**	**High pred. N**	**Low pred. N**
N-1	206 (3.80)	213 (3.90)	209 (4.09)	213 (3.96)
N	191 (3.96)	199 (3.49)	203 (4.19)	213 (4.19)

3.3.3.2 FIXATION-RELATED FNIRS DATA

In analogy to the eye movement data, we report 2 (Frequency of N: High/Low) × 2 (Predictability of N: High/Low) ANOVAs on the basis of [oxy-HB] and [deoxy-HB] for N and N-1 consecutively.

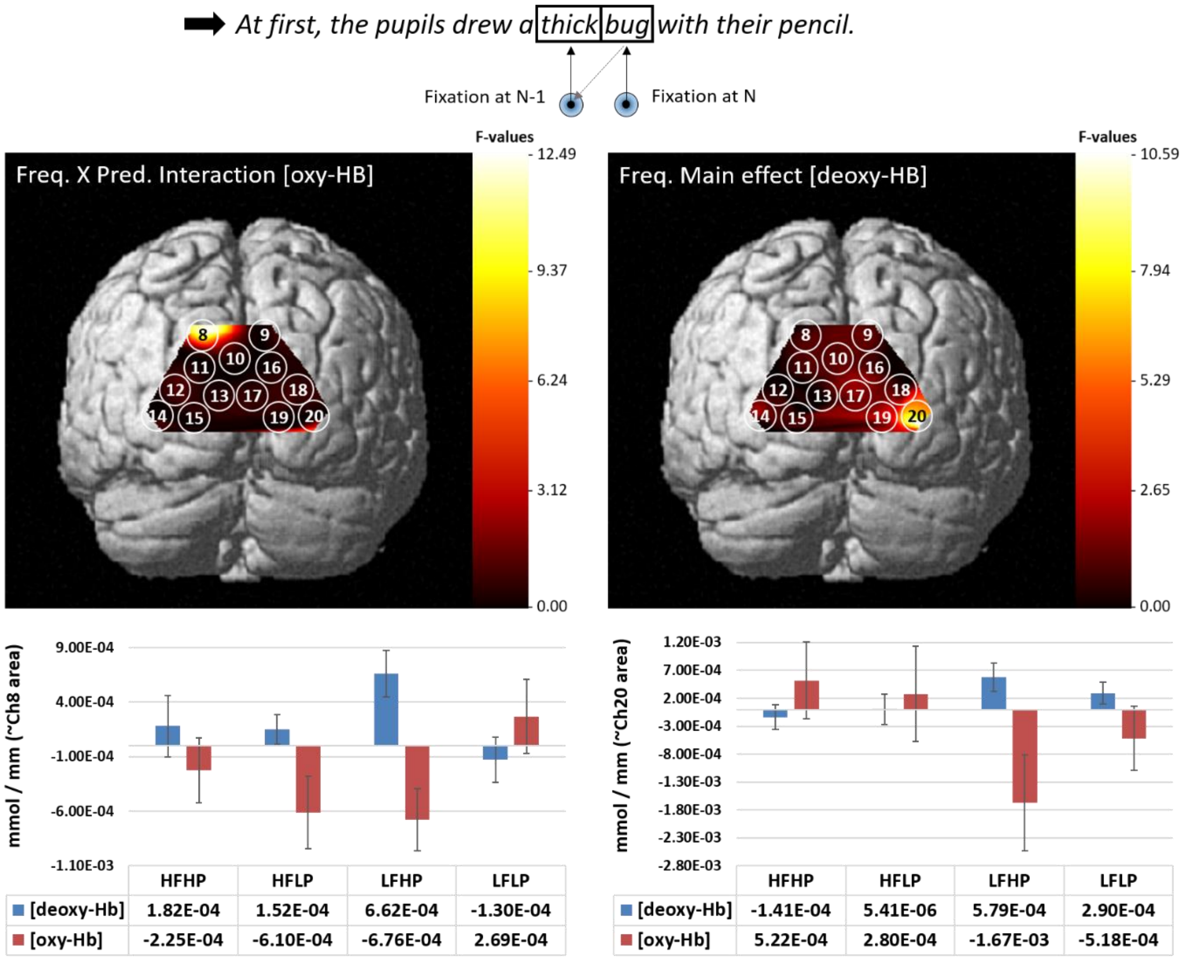
The fixation of N revealed a significant main effect of frequency in the right occipital cortex (probably the ventral V2 region; **Fig. 10** right; Tsuzuki et al., 2007) for [deoxy-HB] ($F(1,35) = 10.59$, $p < 0.0046$) due to more deoxygenated blood for low frequency words. An inversed effect remained for [oxy-HB] in that area ($F(1,35) = 7.67$, $p < 0.01$; **Table 12**). No main effect of predictability of N and no interactions were found at the fixation of the target word.

At the fixation of N-1, we observed no main effects but a significant interaction between frequency and predictability of the subsequent word in the left occipital cortex (probably the dorsal V3 region; **Fig. 10** left; Tsuzuki et al., 2007) for [oxy-HB] ($F(1,35) = 12.49$, $p < 0.0046$). *T*-tests showed that for low frequency words N, a low predictability resulted in increased [oxy-HB] on N-1 when compared to a high predictability (LFLP vs. LFHP: $t(35) = 2.86$, $p < 0.0046$; **Fig. 10** bottom left). An inversed effect was also observable for [deoxy-HB] in the same region ($F(1,35) = 6.1$, $p < 0.01$; **Table 12**).

Generally, no significant changes of activity were observed in the orbitofrontal cortex.

Table 12: *Coupled effects of [oxy-HB] and [deoxy-HB] during the fixation of the manipulated target (N) and its preceding word (N-1). Brain activity increased in the left occipital cortex (V3) at the fixation of N-1 if an infrequent word N was also unpredictable. An increased neural response was revealed in the right occipital cortex (V2) at the fixation of N if it was of low frequency. The columns on the right show the estimated location, MNI-coordinates (Tsuzuki et al., 2007; Ye et al., 2008), the peak F-values, p-value thresholds and signal changes.*

Fixation	Effect	Hemoglobin	Area	MNI	*F*	*P*	Signal changes (mmol / mm)
N-1	Freq. × Pred. of N	[oxy-HB]	Left V3 (~Ch8)	-17 / -92 / 40	12.49	< 0.0046	6.65E-04
		[deoxy-HB]	Left V3 (~Ch8)	-17 / -92 / 40	6.1	< 0.01	-3.81E-04
N	Freq. of N	[oxy-HB]	Right V2 (~Ch20)	35 / -98 / 5	7.67	< 0.01	1.5E-03
		[deoxy-HB]	Right V2 (~Ch20)	35 / -98 / 5	10.59	< 0.0041	-5.02E-04



	HFHP	HFLP	LFHP	LFLP
🟦 [deoxy-Hb]	1.82E-04	1.52E-04	6.62E-04	-1.30E-04
🟥 [oxy-Hb]	-2.25E-04	-6.10E-04	-6.76E-04	2.69E-04

	HFHP	HFLP	LFHP	LFLP
🟦 [deoxy-Hb]	-1.41E-04	5.41E-06	5.79E-04	2.90E-04
🟥 [oxy-Hb]	5.22E-04	2.80E-04	-1.67E-03	-5.18E-04

Fig. 10: *Signal changes at the fixation of N-1 (left) and N (right) due to frequency (HF/LF) and predictability (HP/LP) of N. Left: Interaction of frequency and predictability of N at the fixation of N-1. An upcoming low frequency word resulted in increased activation of the left dorsal occipital cortex if it was of low predictability as well. Right: Main effect of frequency of N at its fixation. The fixation of low frequency words induced an increased activation in the right ventral occipital cortex. Channel positions are overlayed on the activation maps for a better reference to Table 2 and Table 4. The error bars on the bottom reflect standard errors.*

3.3.4 DISCUSSION

We examined hemodynamic responses in the occipital and orbitofrontal cortex to parafoveal and foveal word frequency and predictability effects during natural reading. In contrast to a recent fNIRS study relying on rapid word-by-word presentation (Hofmann et al., 2014; cf. Dambacher et al., 2009), we used a whole sentence reading paradigm with identical stimuli by introducing fixation-related fNIRS.

Eye movement data confirmed previous observations of increased first fixation durations for low frequency and low predictability words at their immediate fixation (e.g. Ehrlich & Rayner, 1981; Inhoff & Rayner, 1986). In addition, when a low frequency word was fixated, we found an increased neural response in the right occipital cortex. At the fixation of N-1, first fixation durations were reduced if the following word N was of high predictability. Fixation-related fNIRS data further indicate a predictability effect for low frequency words: We found increased activation of the left occipital cortex if parafoveal information from the right visual field consisted of an unpredictable low frequency word. No evidence of an involvement of the OFC in evaluating lexical effects could be observed for natural reading.

3.3.4.1 FREQUENCY AND PREDICTABILITY EFFECTS AT THE FIXATION OF THE MANIPULATED TARGET N

We were able to replicate reliable frequency and predictability effects from the eye movement literature (Ehrlich & Rayner, 1981; Inhoff & Rayner, 1986). Longer fixation durations emerged for low frequency (+12 ms) and low predictability (+9 ms; cf. **Table 11**) words. Fixation-related fNIRS revealed converging evidence of increased [deoxy- HB] and decreased [oxy-HB] (Buxton et al., 2004) for low frequency targets in the right ventral occipital cortex (**Fig. 10** right). The first fixation on N was located slightly left from the center on average, representing an optimal viewing position to process critical information, which is contained in the beginning of a word (Bruner & O'Dowd, 1958; Hyönä et al., 1989; O'Regan, 1987; Vitu et al., 2001). The informativeness apparent in the left visual field is probably even more pronounced for capitalized targets, as analyzed in the current study, enhancing the access to higher order information particularly in the right occipital cortex. Moreover, there is evidence of a right-hemispheric dominance during the update of visual input (= remapping) to prepare for upcoming saccades in the extrastriate area (e.g. Mazer & Gallant, 2003; Merriam et al., 2007; Pisella et al., 2011; Saber et al., 2015). Saber et al. (2015) proposed that information for saccade planning is transferred from V2, in which our effect most likely emerged (Tsuzuki et al., 2007), to V4, thus entering the ventral visual stream. Relatedly, Mazer and Gallant (2003) showed that neural activity in V4 is enhanced prior to a bottom-up controlled saccade towards a point of interest. Therefore, we suggest that delayed saccade planning, while reading a difficult word, may be mediated by ventral occipital activation. Because of the relatively low spatial resolution of fNIRS (Zeff et al., 2007), future studies using a method with superior precision (e.g. fixation-related fMRI) may profit from focusing on the occipital region to constrain the exact regions engaged in saccade planning during reading. In addition, a higher sampling rate similar to the current study might help to effectively increase the signal-to-noise ratio (cf. Sabatinelli et al., 2009).

In contrast to Hofmann et al. (2014), our imaging data did not reveal any main effect of predictability at word N. As predictability generally yields smaller behavioral effects in comparison to word frequency (Kliegl et al., 2004), such an effect might be even more difficult to observe consistently in imaging data (cf. Schuster et al., 2016). In addition, other prominent areas that are sensitive to predictability effects (e.g. temporal and inferior frontal cortex; Schuster et al., 2016) were not covered by this study but should be addressed in future research.

3.3.4.2 FREQUENCY AND PREDICTABILITY EFFECTS OF N AT THE FIXATION OF N-1

The present eye movement data suggest that contextual information from the next word can be acquired at a very early time window (Hand et al., 2010; Hawelka et al., 2015; Kliegl et al., 2006; Sheridan & Reingold, 2012). We replicated Hand et al.'s (2010) observation of a decreased first fixation duration prior to the fixation of a predictable word, which can be attributed to a mutual pre-activation of expected words (cf. e.g. Hofmann et al., 2014; Fig. 2 in Radach & Hofmann, 2016). Correspondingly, Snell et al. (2018) concluded that easy-to-process target words reduce the demand of resources during the pre-target fixation. Some studies, however, reported inverted effects of longer fixation durations prior to a predictable word (e.g. Hawelka et al., 2015; Kliegl et al., 2006). This discrepancy might be a result of how skipping behavior was handled in the analyses, as skipping a high predictability word can lead to longer pre-target fixations (Kliegl et al., 2006). Our analyses, however, required the fixation of both, N-1 and N, thus eliminating the influence of skipping. Of further note, behavioral PoF effects have been revealed especially for languages with letter capitalization, like German in the current study (Kliegl et al., 2006; Hawelka et al., 2015; Rayner & Schotter, 2014). Thus, utilizing capitalization as an attentional anchor in the parafovea may have contributed to a significant PoF predictability effect in our eye movement data.

Looking at the current eye movement literature, PoF effects and interactions of frequency and predictability appear rather inconsistent (Degno et al., 2019; Drieghe, 2011; Hand et al., 2010; Himmelstoss et al., 2019; Kretzschmar et al., 2015; Schotter et al., 2012; Sereno et al., 2018; Slattery et al., 2012). Our imaging data suggests further implications for the modelling of eye movement control during reading. On the one hand, processing gradient models are in harmony with our results, as they assume that attention is distributed as a gradient over multiple words around the fixation, indicating parallel processing of foveal and parafoveal words (e.g. Engbert et al., 2005; Reilly & Radach, 2006; Snell et al., 2018). Snell et al.'s (2018) empirical data revealed a similar pattern of increased fixation durations if the next word was of either low frequency or low predictability. They suggested that, in order to reach an activation threshold for successfully recognizing a word, attention probably needs to be broadened if parafoveal information consisted of less pre-activated (and therefore more difficult) words. According to this view, a low frequency word N should result in a wider processing gradient around the fixated word N-1, delaying foveal processing. In our fixation-related fNIRS data, especially infrequent words of low predictability in the parafovea could have induced a broader distribution of attention and therefore increased the neural activity in the left occipital cortex. On the other hand, recent versions of sequential attention shift models (e.g. Reichle et al., 2003, 2009) support lexical PoF effects, especially after Schotter et al. (2014) showed that serial processing does not exclude higher level parafoveal influences during reading: While N-1 is still fixated but finished in processing, attention might shift to N prior to a saccade and enables parafoveal lexical information to affect N-1 at a late stage (Fitzsimmons & Drieghe, 2013; Schotter et al., 2014). Our N-1 words were generally easy to process and fitted well into the context. Therefore, attentional resources were available for the preview of the next word to foster lexical identification. This explanation is also supported by our behavioral finding of a parafoveal predictability effect on the fixation duration of N-1. It is, however, an unresolved issue how sequential models may deal with the interactive lexical PoF effect from our imaging data. In general, an interaction of frequency and predictability provides support for parallel processing. As sequential attention shift models seem to struggle explaining such effects, we agree with Snell and Grainger's (2019) opinion that parallel / interactive processing can be elusive on the surface (= eye movement data), but is readily observable on the basis of hemodynamic responses.

In a lexical decision MEG study by Pernet et al. (2007), foveal target words induced facilitative effects in the left occipital cortex if a prime was presented in the right visual field. They concluded that higher-order lexical information from the parafovea contributes to foveal word processing. Our observed frequency X predictability interaction in that area supports this assumption also for natural reading (**Fig. 10** left). An increased activation in the left dorsal occipital cortex emerged at the fixation of N-1 if a low frequency word N was of low predictability in comparison to a high predictability. We attribute this effect to an upcoming breach of top-down modulated expectation specifically for infrequent words (Sereno et al., 2018). This result appears analogous to the engagement of the OFC for single stimulus presentation (cf. Hofmann et al., 2014; Nobre et al., 1999). Various studies about the hierarchy of time scales in the brain (e.g. Kiebel et al., 2008; Murray et al., 2014; Roesch and Olson, 2005) highlighted the OFC's capability to integrate top-down information into fast decision-making processes to improve the overall performance as evident for unnaturally fast presented unpredictable and rare words (Hofmann et al., 2014). In our present work, we assume that the free visual exploration of a sentence increased the access to bottom-up information which disengaged the OFC to resolve predictive errors. Hence, natural reading allowed the extraction of parafoveal information by activating specifically the dorsal occipital cortex to evaluate breaches of expectation e.g. for the purpose of saccade planning (Merriam et al., 2007; Nakamura & Colby, 2000; Rao & Ballard, 1999; Saber et al., 2015).

3.3.4.3 METHODOLOGICAL CONSIDERATIONS, OUTLOOK AND CONCLUSION

In post-hoc analyses, we further added the distance from the fixation on N-1 to the first letter of N (= launch distance) as factor (**Appendix A** of STUDY C; cf. Hand et al., 2010). In the eye movement data, an interaction of frequency and predictability could be observed at a short launch distance for first fixation durations of N-1 and N (but cf. Slattery et al., 2012). In the fixation-related fNIRS analysis of word N, right occipital neural activation decreased at near launch distances, potentially indicating facilitated visual processing. However, our imaging data did not reveal any three-way interaction of launch distance, frequency and predictability, supporting Slattery et al.’s (2012) concerns of reproducibility.

From a technical perspective, fixation-related fNIRS provides multiple data samples for every fixation on a word at a sufficient spatial resolution to investigate the neural mechanisms of natural reading. In addition, it allows to cross-validate effects of deoxygenated hemoglobin by synchronously measuring tissue oxygenated blood. Concerning studies that coregistered eye movements with EEG during natural reading, even standard frequency effects proved elusive so far, possibly because word predictability dominates the N400 component, while the cause is unresolved for other time windows (Degno et al., 2019; Dimigen et al., 2011; Kretzschmar et al., 2015). Relying on hemodynamics seems to cover such effects, as not only the current study, but also Schuster et al. (2016) found significant changes of brain activity for word frequency.

There are, however, some issues that need to be considered. First, when set up accordingly, fixation-related fMRI can provide a similar temporal resolution as used in this study in addition to a superior spatial resolution (e.g. Lin et al., 2014; Sabatinelli et al., 2009). Second, the medium spatial resolution of fixation-related fNIRS does not allow to make final conclusions about the exact location of our effects (e.g. V2 vs. V3; see **Table 10**). This does not seem to pose a problem for our interpretation, however, as all extrastriate subregions are considered to be involved into saccade planning (Saber et al., 2015). Moreover, our N-1 PoF effect can still be addressed to a more dorsal location, while the frequency effect on N can be related to the ventral extrastriate region most likely. Relatedly, the occipito-temporal and occipito-parietal cortex seem to be strong candidates for further analyses, as our effects were close to their location. We would expect a change of neural activity due to word frequency in the occipito-temporal area, similar to the observation by Schuster et al. (2016). Effects in the occipito-parietal cortex could be explainable in line with the assumption that saliency maps to guide bottom-up attentional shifts (e.g. to the next word) are constructed on the basis of information from V1 leading to the parietal region (Zhang et al., 2012). Therefore, it would be intriguing to replicate the current study via fixation-related fMRI while scanning a single region of interest with only a few slices to improve the temporal resolution, for example (cf. Sabatinelli et al., 2009).

In conclusion, we carried forward the study by Hofmann et al. (2014) and tested if a novel technique, fixation-related fNIRS, can reveal lexical effects during natural reading. We showed that low frequency words increased the activity in the left dorsal occipital cortex prior to their initial fixation only if they were unpredictable, and thus influenced the lexical processing of the preceding word. The immediate fixation of low frequency words engaged the right occipital cortex, suggesting an influence of foveal information from the left visual field for bottom-up driven saccade planning.

3.3.5 APPENDIX A – ANALYSIS OF LAUNCH DISTANCE

Concerning interactive effects of frequency and predictability, we added the distance from the fixation on N-1 to the first letter of N (= launch distance) as post-hoc factor to our eye movement and imaging analyses to examine potentially concealed findings. Launch distances of up to 3 letters were considered as "near" ($M = 1.75$, $SD = 0.84$), and anything above as "far" ($M = 6.03$, $SD = 2.92$; cf. Hand et al., 2010). For N-1 and N fixations separately, we conducted a 2 (Frequency of N: High/Low) × 2 (Predictability of N: High/Low) × 2 (Launch distance from N-1 to N: Near/Far) ANOVA. Three participants were excluded from analyses due to no available data in one of the conditions. As launch distance is not under experimental control, these results should be interpreted tentatively (Slattery et al., 2012).

3.3.5.1 EYE TRACKING DATA

In the analyses on first fixation durations of word N, we found significant main effects of frequency ($F(1,32) = 29.90$, $p < 0.001$, $\eta_p^2 = 0.483$; High: 197 ms, Low: 213 ms), predictability ($F(1,32) = 34.99$, $p < 0.001$, $\eta_p^2 = 0.522$; High: 198 ms, Low: 213 ms) and launch distance ($F(1,32) = 73.32$, $p < 0.001$, $\eta_p^2 = 0.696$; Near: 193 ms, Far: 217 ms; **Table 13**). We also observed a significant three-way interaction of frequency, predictability and launch distance ($F(1,32) = 4.99$, $p < 0.05$, $\eta_p^2 = 0.119$). Resolving the interaction by performing 2 (Frequency of N) × 2 (Predictability of N) ANOVAs at both launch distances resulted in no significant interaction between frequency and predictability (Freq × Pred Near: $F(1,32) = 3.72$, $p = 0.063$, $\eta_p^2 = 0.104$; Freq × Pred Far: $F(1,32) = 1.13$, $p = 0.296$, $\eta_p^2 = 0.034$). *T*-tests still indicated a predictability effect for high frequency words (HFHP vs. HFLP: $t(32) = -4.83$, $p < 0.001$) but not for low frequency words (LFHP vs. LFLP: $t(32) = -1.75$, $p = 0.089$) if the launch distance was small.

For first fixation durations of word N-1, a significant PoF main effect was observed for predictability ($F(1,32) = 6.61$, $p < 0.05$, $\eta_p^2 = 0.159$; High: 211 ms, Low: 216 ms) and launch distance ($F(1,32) = 7.33$, $p < 0.05$, $\eta_p^2 = 0.173$; Near: 210 ms, Far: 217 ms), but not for frequency ($F(1,32) = 1.58$, $p = 0.217$, $\eta_p^2 = 0.043$; High: 212 ms, Low: 215 ms; **Table 13**). There was a significant three-way interaction of frequency, predictability and launch distance ($F(1,32) = 4.20$, $p < 0.05$, $\eta_p^2 = 0.107$). 2 (Frequency of N) × 2 (Predictability of N) ANOVAs at both launch distances revealed a significant interaction of frequency and predictability at a near launch distance only (Freq × Pred Near: $F(1,32) = 5.66$, $p < 0.05$, $\eta_p^2 = 0.139$; Freq × Pred Far: $F(1,32) = 0.77$, $p = 0.387$, $\eta_p^2 = 0.021$): When the launch distance between N-1 and N was near, *t*-tests indicated a significant PoF predictability effect for low frequency (LFHP vs. LFLP: $t(32) = -2.64$, $p < 0.05$) but not for high frequency words (HFHP vs. HFLP: $t(32) = -0.24$, $p = 0.813$). All other interactions were not significant.

Table 13: *Mean first fixation duration (in ms) of the experimental conditions including launch distance (LD) as additional post-hoc factor. Standard errors are provided in parentheses.*

		High frequency N		Low frequency N	
Fixation	**LD**	**High pred. N**	**Low pred. N**	**High pred. N**	**Low pred. N**
N-1	Near	208 (3.80)	209 (3.92)	205 (4.65)	218 (4.08)
	Far	212 (4.33)	219 (4.40)	218 (5.62)	220 (4.53)
N	Near	171 (4.25)	199 (5.74)	196 (5.20)	208 (6.29)
	Far	206 (4.50)	214 (3.56)	218 (4.50)	230 (4.06)

3.3.5.2 FIXATION-RELATED FNIRS DATA

Imaging data suggests a main effect of launch distance with increased [deoxy-Hb] ($F(1,32) = 9.75$, $p < 0.0046$) and decreased [oxy-Hb] ($F(1,32) = 11.18$, $p < 0.0046$) at a near launch distance in the right ventral occipital cortex (**Fig. 11**). In addition, frequency of N interacted with launch distance in the same area ([oxy-Hb]: $F(1,32) = 6.11$, $p < 0.05$; [deoxy-Hb]: $F(1,32) = 9.13$, $p < 0.0046$). At a far launch distance, [deoxy-Hb] increased for low frequency words (LFfar vs. HFfar: $t(32) = 2.61$, $p < 0.01$). If the distance between the fixation on N-1 and N was near, however, [deoxy-Hb] showed a reduction at the fixation of an infrequent word N (LFnear vs. HFnear: $t(32) = -2.66$, $p < 0.01$).

No significant main effects were found for the N-1 analysis, but a significant interaction of frequency and predictability was observable in the left dorsal occipital cortex for [oxy-Hb] ($F(1,32) = 12.38$, $p < 0.0046$; **Fig. 12**). When the following word was of low frequency, a low predictability resulted in increased [oxy-Hb] at the fixation of N-1 (LFLP vs. LFHP: $t(32) = 2.35$, $p < 0.0046$). An inversed effect of this interaction was also revealed for [deoxy-Hb] ($F(1,32) = 6.67$, $p < 0.01$). All other interactions were not significant.

Fixation at N

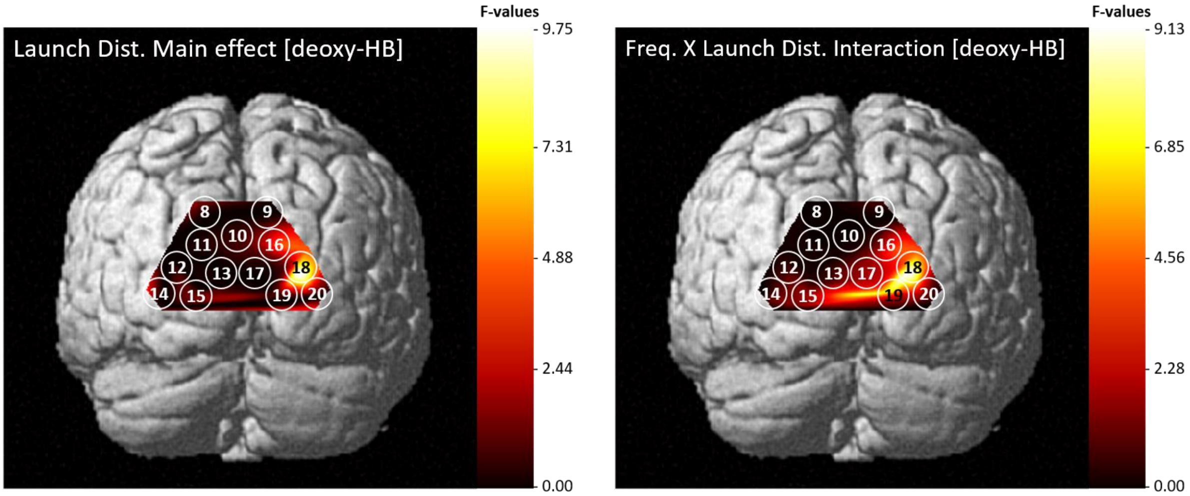


Fig. 11: *Signal changes at the fixation of N. Left: Main effect of launch distance. A close distance between N-1 and N resulted in increased activation of the right ventral occipital cortex. Right: Interaction of frequency of N and launch distance. Activation in the right ventral occipital cortex increased if a low frequency word was preceded by a long saccade. Channel positions are overlayed on the activation maps for a better reference to* **Table 10**.

Fixation at N-1

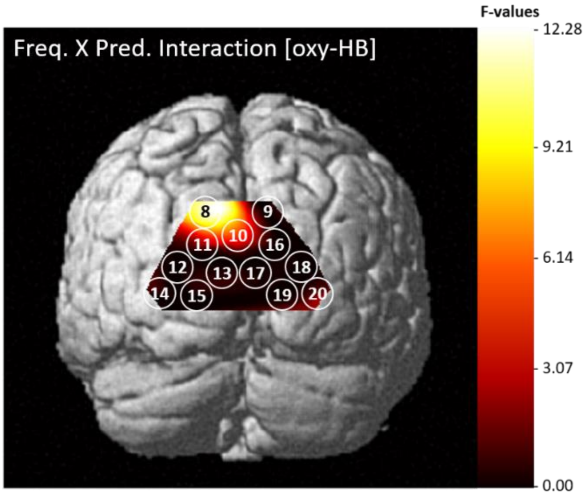


Fig. 12: *The fixation of N-1 revealed signal changes of frequency of N in interaction with predictability of N, independently of launch distance. An upcoming low frequency word resulted in increased activation of the left dorsal occipital cortex if it was of low predictability as well. Channel positions are overlayed on the activation maps for a better reference to* **Table 10**.

4 GENERAL DISCUSSION

4.1 SUMMARY OF THE KEY FINDINGS

The current thesis adds sustainable value to the research on single word and whole sentence processing by introducing novel computational approaches and neuroimaging methodologies in three cumulative studies.

STUDY A examined the dissociability of associative and semantic priming on the basis of word co-occurrences. Previous priming research often relied on subjective measures to determine the relation of two words, which offered no clear separation of direct association and semantic similarity. Lucas (2000) argued that pure semantic priming can be evoked by using prime-target pairs of the same category. Associative priming, on the other hand, did not seem to exist without any semantic overlap. By calculating associative and semantic relations from a sentence corpus, STUDY A showed that this relatively simple approach of counting word co-occurrences allows the prediction of both priming types. In line with the literature, the priming effect of directly associated words was stronger as SOA increased, while semantic priming was present only at a short SOA. By constructing a full-factorial manipulation of direct association and semantic similarity, this study addressed the challenge to find pure associative relations, and demonstrated a strictly additive behavior of the two priming types. Finally, the findings of STUDY A are relevant for performance tuning of the AROM to simulate implicit and explicit semantic memory tasks.

STUDY B investigated the functional connectivity of brain regions (specifically targeting the LIFG) during semantic competition, and related the observations to the model-to-brain-data proposal by Hofmann and Jacobs (2014). Breaches of semantic expectation resulted in increased activation of the LIFG, the superior frontal gyrus, the occipital cortex, the precentral gyrus, the ACC and the MTG. PPI analysis revealed an interaction of the LIFG to the anterior fusiform gyrus, the hippocampus, the OFC, the ACC and the cerebellum when semantic conflicts had to be resolved. The functional dependency of the LIFG and the fusiform gyrus can be related to the connectivity assumption of the orthographic and the semantic layer in the AROM. The connectivity of the LIFG to the OFC and ACC can be interpreted as evidence for a top-down control mechanism, which detects semantic mismatches and returns feedback to the LIFG. The direct link of the LIFG and the hippocampus implies the filtering of semantic information (pattern separation) when evaluating between semantic expectancies and semantic mismatches. It further provides testable evidence for the idea of an additional hippocampal layer in the AROM (Hofmann & Jacobs, 2014; cf. Kumaran & McClelland, 2012).

STUDY C looked at the lexical processing during whole sentence reading by employing a novel technique, fixation-related fNIRS. The parallel processing of words from the parafovea was disregarded for a long time due to inconclusive empirical evidence (see Angele et al., 2015; Reichle et al., 2009;

Schotter et al. 2012). Furthermore, occasional findings of interactive lexical effects led to discussions, as they would challenge the view of strictly additive effects of word frequency and predictability (cf. Staub, 2015). These debates recently encouraged researchers to coregister eye movements with neuroimaging data. STUDY C was able to replicate standard findings of the eye movement literature (longer fixations on unpredictable and infrequent words), while neuroimaging data revealed an interactive lexical PoF effect in the left occipital cortex. The left occipital cortex was increasingly activated only if the following word was of low frequency and low predictability. It is likely that a very difficult word in the parafovea caused a delay in saccade preparation to deal with the increased cognitive demand, e.g. by re-programming the saccade into a regressive eye movement for re-evaluation of the previous words. In contrast to a similar study by Hofmann et al. (2014), which presented the same sentences word-by-word, no difference in OFC activation was observable. The top-down control exerted by the OFC was most likely not as critical for natural reading, where fixations are self-paced. Hence, the occipital cortex could manage the timing of saccades without support from the OFC.

The following sections include a discussion on the key findings and their implications for future research. They further provide additional analyses, such as a comparison of behavioral data to simulations by the AROM, and contain a critical examination of the limitations.

4.2 WORD CO-OCCURRENCES AS PREDICTOR OF ASSOCIATIVE VARIABLES

STUDY A successfully showed that computationally determined word co-occurrences can explain different priming phenomena. If two words are often used in the same context (= direct association), the brain can form a specific neural response to their co-occurrence. Hence the phrase "what fires together, wires together" (Hebb, 1949). Transferred to an implicit priming task, the presentation of a prime activates the neural representations of likely target words. On that basis, the spreading activation theory suggests that a very strong prime-target connection results in a faster and more pronounced pre-activation of the target (Anderson, 1983; Collins & Loftus, 1975; Quillian, 1967). The recognition of a directly associated target word is further improved at longer SOAs due to the accumulated pre-activation (McNamara, 2005; Neely, 1991). Accordingly, co-occurrence based direct associations revealed exactly such findings. Relating semantic relationships to the number of common associates was discussed by McKoon and Ratcliff (1992), and tested by Rapp (2002). Again, the results of STUDY A provide evidence for this definition. Facilitation by a prime with many common associates to the target occurred at the short SOA, only, which matches the standard observations in the semantic priming literature.

But why are semantic relations affected by inhibition during strategic processing, and direct associations are not? Here, the co-occurrence based approach together with the spreading activation theory might provide a solid explanation. When a prime is presented, activation first spreads to its direct neighbors in the semantic network and then to its indirect connections. Hence, associative (via direct connections) and semantic (via indirect connections) priming can occur at short SOAs due to the automatic spread of activation. At long SOAs, semantic expectancy (the prediction of the target based on pre-activation, before seeing the target) and semantic matching (the search of the target word in the semantic network, after seeing the target) determine the amount of facilitation or inhibition (McNamara, 2005; Neely, 1991). McNamara (2005) suggested that the predominantly inhibitive effect of semantics at long SOAs is connected to the search for the semantic match among all pre-activations by the prime. Prime-target pairs with a strong semantic similarity share many associates, and are thus predominantly related via these nodes in the semantic network (Rapp, 2002). As a result, semantic matching has to go one level deeper into the network, which increases the cognitive demand drastically when strategic processes are involved. On the other hand, if the prime and the target are directly associated, the target may profit from the prime also at a long SOA because only immediate neighbors in the network have to be compared, which is faster and less exhausting.

4.3 DOES PURE ASSOCIATIVE PRIMING EXIST?

The purity of the priming types was investigated in two extensive meta-analyses by Lucas (2000) and Hutchison (2003). Both concluded that a pure semantic relationship between two words can be acquired by carefully selecting words from e.g. the same category. Transferred to word co-occurrences, this statement assumes that both words do not appear together in the same sentence, but can (under optimal conditions) be replaced with each other without changing the meaning (e.g. THIEF – BURGLAR). The possibility of directly associated words with no semantic relation was put into question by Lucas (2000) and McNamara (2005), mainly because the usually applied free association norms cannot exclude semantic influences.

For instance, Ferrand and New (2003) attempted to disentangle associative from semantic priming by utilizing such norms. This resulted in “pure” associative combinations like SPIDER and WEB. By the definition of word co-occurrences however, SPIDER and WEB would not be entirely free of semantics, as e.g. SILK is a shared (and strong) direct associate of both words. Moreover, their priming effects were rather atypical to the usually observed pattern. “Pure” semantic priming decreased slightly at longer SOAs, but remained significant. “Pure” associative priming decreased at a long SOA, thus opposite to the priming literature. In addition, they did not control for word frequency over both conditions, which makes their findings very hard to interpret.

Hutchison (2003) suggested that mediated associates can induce pure associative priming. In his example, LION should prime STRIPES via their direct connection to TIGER. However, the co-occurrence based approach would not consider LION to be directly associated with TIGER but indirectly, as they are semantically related and can be replaced in many contexts. Thus, the relation between LION and STRIPES seems much more distant, and in fact based on a direct association between TIGER and STRIPES and a semantic relation between TIGER and LION. This further contradicts with the definition of associative priming, which should rely on direct and not indirect connections in the priming literature (cf. McNamara, 2005). Together with the fact that mediated priming occurs only at short SOAs (Hutchison, 2003), it seems that mediated priming is a special case of priming, which behaves more like semantic priming.

By investigating computationally calculated word co-occurrences, Rapp (2002, p. 7) proposed that purely directly associated words (also referred by him as “1st-order” or “syntagmatic”) and purely semantically related words (also referred by him as “2nd-order” or “paradigmatic”) should exist: “Whereas the results of the 2nd-order computation are of paradigmatic type exclusively, those of the 1st-order computation are a mixture of both syntagmatic and paradigmatic associations. Removing the 2nd-order associations from the 1st-order associations leads to solely syntagmatic associations”. This means that computations of direct association include its pure form and a form with semantic influences. The latter type likely reflects priming with an "associative boost" (Lucas, 2000), which has usually been investigated when using free association norms. By looking at the computations of pure direct associations, one should be able to clearly separate associative from semantic priming. Thus, STUDY A employed pure direct associations probably for the first time in a primed lexical decision task. Stimulus selection of STUDY A revealed that many purely directly associated word pairs often appear together in idioms, like *"The DEVIL is in the DETAIL"* or "*A SHIVER ran down his SPINE*". Hence, they co-occur very frequently, but mostly within the identical syntactical structure. In such cases, STUDY A always used the first noun (e.g. SHIVER) to prime the second (e.g. SPINE). This implies that the pure associative priming effect – as investigated in the current thesis – could have been modulated by forward associations to some extent. Chwilla et al. (1998) compared the priming effects of bidirectional and unidirectional (forward and backward separately) associations. They observed similar priming effects for bidirectionally associated words and (noncompound) words with forward associations (60 ms vs. 61 ms, collapsed across the SOAs). Forward priming of noncompound words was significantly stronger than backward priming (61 ms vs. 27 ms). The pure direct associations in STUDY A were roughly 40% forward directional and 60% bidirectional. Based on the observations of Chwilla et al. (1998), it is safe to assume that both types contributed equally to the pure associative priming effect. The priming effect could have been weaker if mainly backward associations were used, however. This might have implications for the proposal in STUDY A that direct associations and semantic similarity contributed additively to the priming effect. Under the additive assumption, the sum of pure associative and semantic priming should be equal to the priming by words with a direct and a semantic relation. As the priming effect might differ for backward associations, the additivity could turn into over- or under-additivity, which needs to be considered in future research.

4.4 INFLUENCE BY ASSOCIATIVE / SEMANTIC COHESION ON THE PRIMING RESULTS

One criticism of STUDY A (and to some extent STUDY B, as both used the identical stimuli) may be that stimulus creation and the statistical analyses did not account for associative or semantic cohesion. As demonstrated for recognition memory tasks by Stuellein et al. (2016), a high associative cohesion allowed a more accurate recognition for studied words, and evoked more errors for newly presented words. Also in priming tasks, a high semantic cohesion can facilitate the target recognition (Wible et al., 2006). Critically, STUDY A proposed evidence for the dissociation of the two types of relationships, which were either more effective at the short (semantics) or the long SOA (direct associations). A significant interaction with the associative / semantic cohesion could hamper this assumption, as the increased priming effect at the long SOA by direct associations (or the inhibitive effect by semantic relations) could have been a result of an imbalanced cohesion. Moreover, if associative cohesion was not controlled for a high and low semantic similarity, or semantic cohesion not matched for the factor direct association, no final conclusions could be drawn concerning their dissociability.

In a post-hoc correlation analysis, neither associative nor semantic cohesion were correlated to a critical level with direct association (associative cohesion: $r = 0.162$; semantic cohesion: $r = 0.004$) or semantic similarity (associative cohesion: $r = -0.009$; semantic cohesion: $r = 0.240$). Next, post-hoc 2 (direct association: strong/no) × 2 (common associates: many/no) × 2 (SOA: 200/1,000 ms) by-items ANOVAs with the associative and semantic cohesion of the target words as dependent variables were conducted.

The ANOVA on associative cohesion revealed a significant main effect for the direct association of prime and target ($F_2(7, 199) = 4.35$, $p < 0.05$, $\eta_p^2 = 0.022$). Thus, target words with a strong direct association to the prime also had significantly more direct associates within the stimulus set. All other main effects and interactions were highly insignificant.

The ANOVA on semantic cohesion showed a significant main effect for common associates ($F_2(7, 199) = 11.72$, $p < 0.001$, $\eta_p^2 = 0.058$). If the prime and target were semantically similar, the target further had a high semantic overlap to the other target words. Again, all other main effects and interactions remained insignificant.

Importantly, both types of cohesion affected only the same type of prime-target relation. In addition, associative and semantic cohesion did not interact with SOA in any way. Thus, the cohesion might have affected the main effect sizes of direct association and semantic similarity in STUDY A, but not the crucial observations regarding their interaction with SOA, or their separable distribution to the priming effect.

4.5 PREDICTING PRIMED LEXICAL DECISIONS WITH THE AROM

Lucas (2000) argued that spreading activation models perform rather poorly in predicting priming effects. Such models rely on associative relationships, while pure semantics seem to be the preferred predictor. Hutchison (2003), on the other hand, pointed out that semantic relationships are covered by the co-activation of shared associates, which indirectly lead to a stronger activation of the target word.

While IAMs were initially not designed to account for associative (priming) effects, the AROM introduced a semantic layer based on co-occurrence statistics. During the setup of the semantic layer, every associated word pair receives a positive value, which corresponds to the co-occurrence based direct association (see section 1.1 for more details). If two words are not associated, their initial value is slightly negative to induce an inhibitive effect on one of these words if the other is presented. This initial state can be regarded as a representation of the semantic long-term memory. When a prime is processed by the model, excitatory activation in the semantic layer spreads from the prime to its direct associations and to their subsequent associates, resulting in their pre-activation. Therefore, associative (pre-activation of direct connections) and semantic (pre-activation of shared associates) priming should be addressable, as proposed by Hutchison (2003).

The following paragraphs highlight some AROM simulations of the semantic priming experiment conducted in STUDY A to compare the behavioral data with the model data. The lexicon of the model consisted of 9530 German nouns. Their individual frequency class modulated the initial activation in the orthographic layer, as a high frequency word should be more salient than an infrequent word. The direct association values between all words from the lexicon were added to the semantic layer (cf. Quasthoff et al., 2006; Rapp, 2002). One processing step (further referred to as "cycle") in the AROM corresponded to 50 ms of real time. Hence, the prime was presented for three cycles (= 150 ms), followed by one (= SOA of 200 ms) or seventeen cycles (= SOA of 1,000 ms) of no stimulus display[5]. Next, thirty cycles (= 1,500 ms) were allowed for the target identification. In every cycle, the activation in the layers was updated according to the pre-determined inhibitory and excitatory connections; within and between the layers (**Fig. 2**; also see Hofmann et al., 2011; Hofmann & Jacobs, 2014). Concerning the free parameters of the network, the excitation (α) from the orthographic to the semantic layer was set to $\alpha = 0.09$, and from the semantic to the orthographic layer to $\alpha = 0.12$. Within the semantic layer, direct associations of the stimulus received an excitation of $\alpha = 0.15$, while

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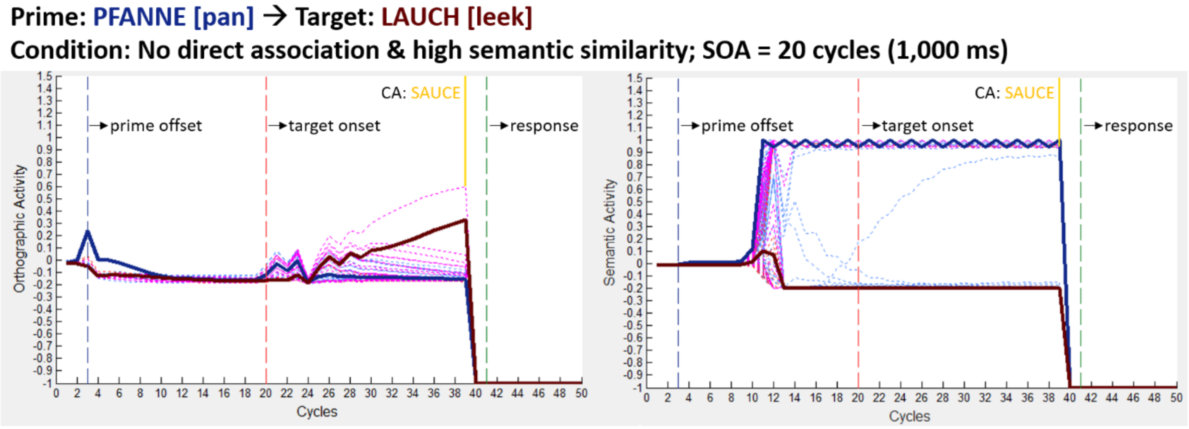
[5] A different approach would be to keep presenting the prime for the full duration of the SOA, instead of showing no stimulus for one or seventeen cycles. This would help the model to preserve activation on all the associated words. The behavioral data of STUDY A is based on a blank screen for that duration, however. Thus, the prime was presented to the model for three cycles only, followed by no stimulus display for one or seventeen cycles. The implications of these two approaches will be addressed in the discussion below.

unrelated words were inhibited (γ) by γ = -0.09. The decay of activation in the semantic layer was set to 0.06. The minimal change of activation in that layer was -0.2. The target stimulus was considered to be correctly identified if its activation in the orthographic layer reached a value of 0.6 or greater (further referred to as "breakcycle")[6]. All other parameters were inherited from the latest implementation by Hofmann and Jacobs (2014).

Similar to human behavior, the model sometimes identified the wrong target word because of orthographic or semantic similarities (e.g. GESICHT [face] instead of the orthographic neighbor GEWICHT [weight]; or SAUCE [sauce] instead of the semantic neighbor LAUCH [leek]). **Fig. 13** shows the model data of PFANNE [pan] priming LAUCH [leek]. The two words have no significant direct association but a high semantic similarity, according to co-occurrence statistics. The long SOA caused the false identification of the target word presumably due to the pre-activation of semantically similar words like SAUCE. In addition, the German words LAUCH and SAUCE differ only in the first and last letter from each other, making a discrimination even harder for the model.

Analogous to the behavioral data, incorrect trials, such as the example above, were excluded from further analyses, as well as when no word reached the activation threshold of 0.6 after thirty cycles (= no response).



Prime: PFANNE [pan] → Target: LAUCH [leek]
Condition: No direct association & high semantic similarity; SOA = 20 cycles (1,000 ms)

Fig. 13: *Model data (left: activity in the orthographic layer; right: activity in the semantic layer) from the prime-target pair PAN (bold blue line) and LEEK (bold red line). The dotted blue curves correspond to direct associates of PAN; the dotted red curves refer to direct associates of LEEK. PAN and LEEK share many direct associates (the dotted purple curves) such as SAUCE (marked in yellow), but rarely appear in the same sentence. The long SOA allowed the pre-activation of many direct associates of the prime PAN. This resulted in a suppression of the target LEEK in the semantic layer (see bold red curve on the right). The common associate (CA) SAUCE received a strong orthographic and semantic activation, and was incorrectly identified as the target stimulus.*

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[6] All credits for parameter optimization of the semantic priming paradigm go to Markus J. Hofmann.

Fig. 14 compares the behavioral data with the model data, which significantly correlate by $r = 0.190$ ($p < 0.05$). Coincidently, word pairs with a strong associative and semantic relation were identified the fastest. It is most striking that facilitative pure associative priming did not occur at the long SOA in the model data, while pure semantic priming followed the assumption of a facilitative effect at a short SOA only (cf. **Table 3**). For further investigation, a 2 (Direct association: Strong/No) × 2 (Semantic similarity: High/No) × 2 (SOA: Short/Long) by-items ANOVA with breakcycle as dependent variable was performed.

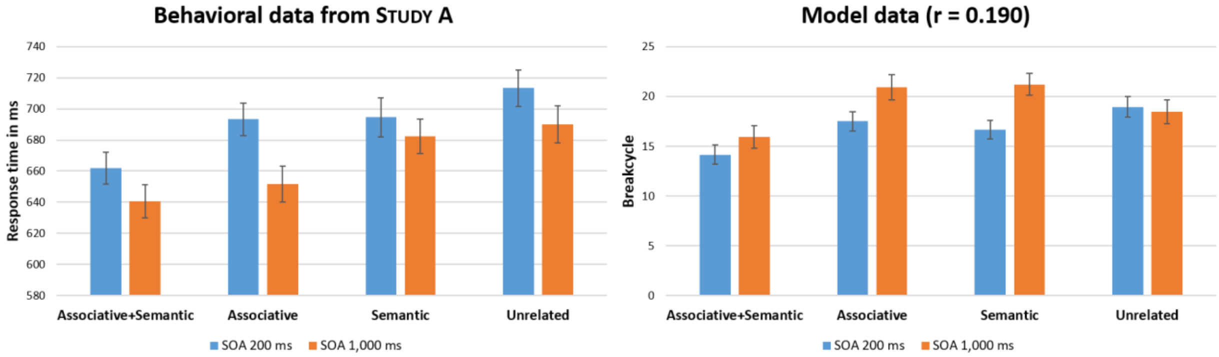


Fig. 14: *Mean response times per condition from Study A (left) in comparison with the mean breakcycles from the model data (right). The error bars reflect standard errors.*

The 2 × 2 × 2 ANOVA revealed main effects for direct association ($F_2(1, 153) = 4.86$, $p < 0.05$, $\eta_p^2 = 0.032$; Strong: 17.13 cycles, No: 18.83 cycles), semantic similarity ($F_2(1, 153) = 6.53$, $p < 0.05$, $\eta_p^2 = 0.043$; High: 16.99 cycles, No: 18.96 cycles) and SOA ($F_2(1, 153) = 9.06$, $p < 0.05$, $\eta_p^2 = 0.058$; Short: 16.82 cycles, Long: 19.14 cycles). Moreover, direct association interacted significantly with semantic similarity ($F_2(1, 153) = 8.19$, $p < 0.05$, $\eta_p^2 = 0.053$). A high semantic similarity reduced the breakcycle only if a strong direct association was likewise present ($t(153) = -3.77$, $p < 0.001$). Finally, a slightly significant three-way interaction of direct association, semantic similarity and SOA ($F_2(1, 153) = 4.75$, $p < 0.05$, $\eta_p^2 = 0.032$) indicates that the interaction of direct association and semantic similarity was a little stronger at the short SOA ($t(153) = -3.02$, $p < 0.01$) than at the long SOA ($t(153) = -2.21$, $p < 0.05$). All other interactions were insignificant.

Lucas' (2000) concern whether spreading activation models can address semantic relationships was already dismissed by Hutchison (2003) and Rapp (2002) from a more theoretical point of view, as shared direct associates should reflect the quantity of the semantic overlap. The results of the 2 × 2 × 2 ANOVA further challenge Lucas' (2000) opinion, and provide evidence that such models can account for both, associative and semantic priming. There are, however, some notable differences between the model and the empirical data.

First, the main effect of SOA was reversed for the model data. Instead of a facilitated target recognition at a long SOA, it took significantly longer. It seems as if this issue is related to the option of presenting the prime for the full duration of the SOA to the model, or including a blank phase (see **Footnote 5**). In this regard, Hofmann (2021) reported reduced breakcycles at the long SOA without modelling a blank phase. In the present simulation however, activation in the orthographic and the semantic layer was allowed to decline for seventeen cycles (long SOA) during the blank phase. Thus, even though the targets were selected to be one of the top associates of the prime, competition by some stronger co-activated words probably suppressed the target. Consequently, more cycles were required to push the target up to the threshold for a successful identification.

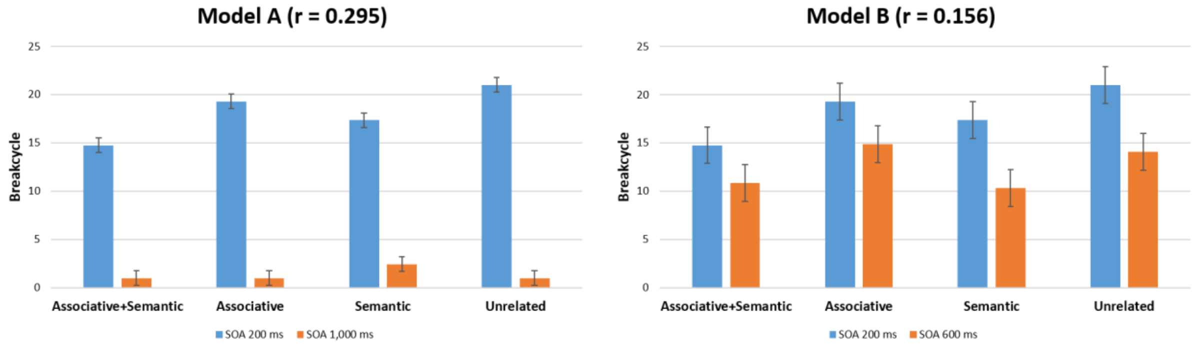


Fig. 15: *Mean breakcycles per condition when showing the prime for the full duration of the SOA (no blank phase). Model A (left) used identical SOAs as Study A (200 ms and 1000 ms), while Model B (right) used a long SOA of 600 ms instead of 1,000 ms. The error bars reflect standard errors.*

For a comparison, **Fig. 15** shows the modelling data when presenting the prime until the onset of the target. This allowed the prime to exert pre-activation until the target onset, which reduced the average breakcycle at the long SOA. Critically, this approach also exposed some inherent flaws of that version of the model. An SOA of 1,000 ms (=20 cycles of prime presentation) resulted in an immediate break of the simulation after the target appeared in many cases (**Fig. 15** left). In addition, almost all targets were incorrectly recognized at the long SOA (> 95%). It looks like the co-activated non-target stimuli dominated over the target word, and reached the activation threshold even before the target processing started. By reducing the duration of the long SOA to 600 ms (=12 cycles of prime presentation) less dominant co-activations by the prime were observable (**Fig. 15** right). Still, a lot of the target words were not correctly recognized (> 70%).

Another flaw is related to the explained variance of the models. Judging by the values, Model A in **Fig. 15** should perform the best, in comparison to Model B in **Fig. 15** and the original model highlighted in

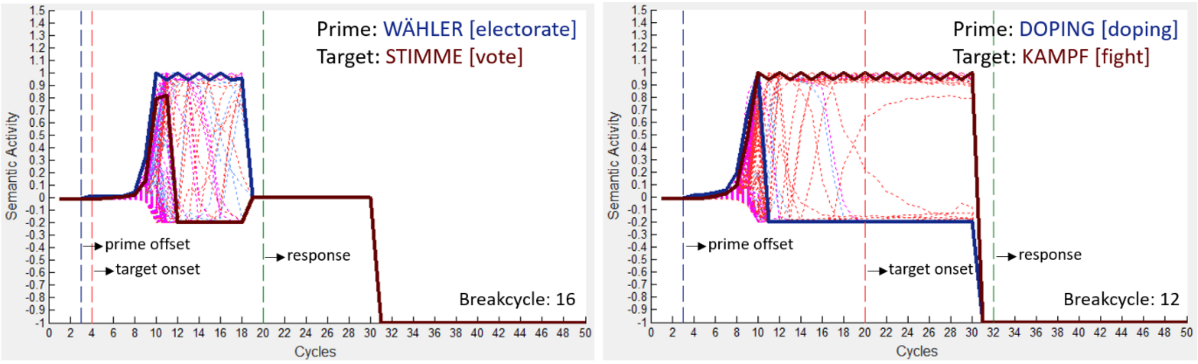
Fig. 14. Just by looking at the data however, it becomes obvious that the other two models represent the empirical data more plausibly.

In sum, this work-around allowed to account for the SOA effect of the empirical data, but created more issues than it resolved. Moreover, it does not fully match the procedure in STUDY A, which included a blank phase between prime and target. A possible solution for this issue could be to implement a recurrent mechanism to maintain semantic (co-)activation by the prime during the blank phase. In this light, STUDY B revealed a functional connectivity of the semantic network to the hippocampus during primed lexical decisions. The hippocampus contains a recurrent system when encoding new episodic and semantic information, which also seems to be activated during semantic priming tasks to filter relevant from irrelevant information (e.g. Kumaran & McClelland, 2012; O'Reilly et al., 2014; Ranganath & Ritchey, 2012). It would therefore be biologically plausible to include such a routine to the model to circumvent a too effective drop of prime-target activation for SOAs with a long blank phase. The following section 4.6 picks up on this proposal.

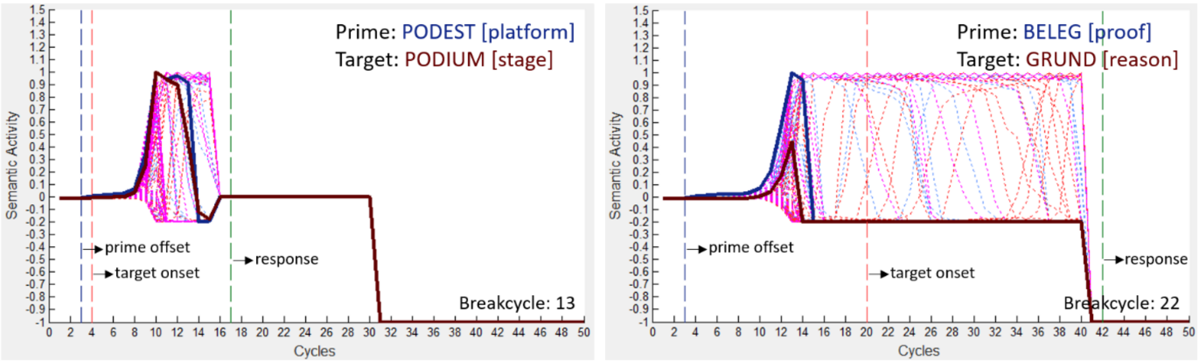
Presumably as a consequence of a generally delayed target recognition at long SOAs, the model of **Fig. 14** predicted no interaction between direct association and SOA ($F_2(1, 153) = 0.13$, $p = 0.716$, $\eta_p^2 = 0.001$). In fact, the priming effect by direct association was even slightly reduced at the long SOA, thus inverted to the empirical data (priming by direct association: 1.98 cycles at the short SOA versus 1.42 cycles at the long SOA; cf. **Table 3**). This contradicts with the spreading activation theory for direct associations, which assumes facilitation over time (Collins & Loftus, 1975; Quillian, 1967). For a selection of directly associated stimuli, a long SOA still facilitated the target as expected. For instance, it took 16 cycles to correctly identify VOTE after a short SOA, and 12 cycles to recognize FIGHT after a long SOA (see **Fig. 16a**).

Also the interaction between semantic similarity and SOA disappeared in the model data ($F_2(1, 153) = 1.20$, $p = 0.275$, $\eta_p^2 = 0.008$). Descriptively however, there was a more positive effect by semantic similarity at the short SOA (priming by semantic similarity: 2.81 cycles at the short SOA versus 1.12 cycles at the long SOA), which is in line with the empirical data, as semantic competition should increase at longer SOAs (cf. **Fig. 16b** and **Table 3**). This suggests that semantics were less affected by the issue of a long blank phase, as this inhibitive influence by competing semantically similar words during a longer processing period is a standard finding in the priming literature (e.g. McNamara, 2005).

a) Strong direct association & no semantic similarity



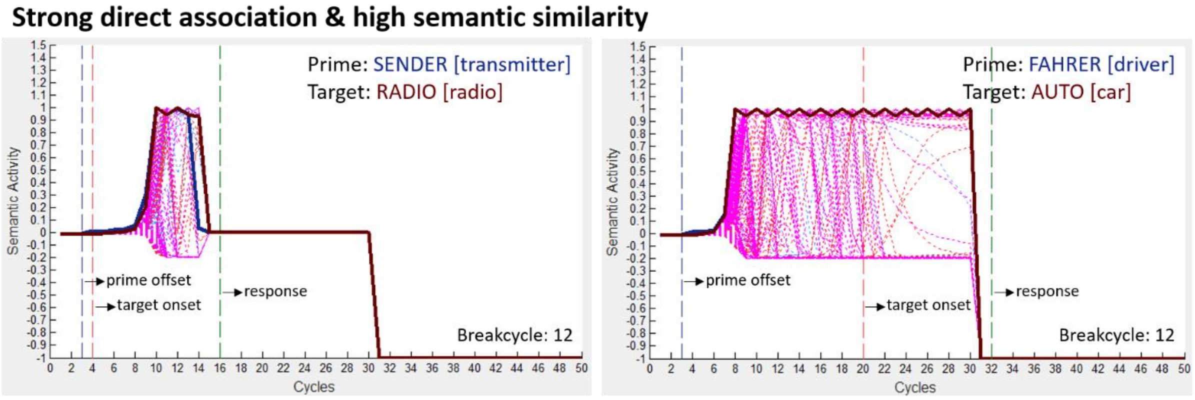
b) No direct association & high semantic similarity



SOA = 4 cycles (200 ms) SOA = 20 cycles (1,000 ms)

Fig. 16: *Examples for an optimal activation behavior in the semantic layer of the AROM for a) purely directly associated and b) purely semantically related prime-target pairs at short (left) and long (right) SOAs. Pure direct associations should be increasingly facilitated at a long SOA (21 versus 12 cycles), while pure semantic relations should receive inhibition at a long SOA (13 versus 22 cycles). Bold blue curve = prime; bold red curve = target; dotted blue curves = direct associates of the prime; dotted red curves = direct associates of the target; dotted purple curves = common associates.*

Possibly also related to the issue above, the model favored an overadditive relation of direct association and semantic similarity, while the empirical data strongly suggests their additivity (see Study A). The model data in **Fig. 14** shows that target words with a strong direct association and a high semantic similarity to the prime were recognized much earlier than targets from the other conditions at both SOAs. This would be perfect evidence for the associative boost theory proposed by Lucas (2000), but not be in line with the findings of Study A. Moreover, the model predicted diverging influences by the combination of direct association and semantic similarity at the two SOAs (hence the three-way interaction). As exemplified in **Fig. 17**, some targets with a strong associative and semantic relation to the prime were able to overcome any conflicts exerted by co-activated words with similar effectiveness at both SOAs. Overall however, priming in this condition was more effective at the short SOA (priming by direct association and semantic similarity: 4.79 cycles at the short SOA versus 2.54 cycles at the long SOA). This is different to the empirical data of Study A, which revealed equally strong priming effects at both SOAs (50 ms versus 51 ms; cf. **Table 3**).



SOA = 4 cycles (200 ms)

SOA = 20 cycles (1,000 ms)

Fig. 17: *Example model data for prime-target pairs with a strong direct association and a high semantic similarity at a short (left) and at a long (right) SOA. Under optimal conditions, the target should be identified very fast at both SOAs (here 12 cycles). Bold blue curve = prime; bold red curve = target; dotted blue curves = direct associates of the prime; dotted red curves = direct associates of the target; dotted purple curves = common associates.*

In conclusion, the simulation of the behavioral findings in STUDY A allowed the prediction of associative and semantic priming, but struggled with the influence by SOA due to the relatively strong decay of target pre-activation during a long blank phase. As a general reduction of the decay rate parameter might result into too early decisions and less time for (semantic) word competition to unfold (Hofmann et al., 2011; McClelland & Rumelhart, 1981), it would be biologically more plausible to add a recurrent system to the AROM. Thus, target pre-activation could idle on a higher level for a short period of time.

4.6 IMPLICATIONS OF BRAIN DATA ON THE CONNECTIVITY ASSUMPTIONS OF THE AROM

While neurocognitive models are often opted to explain as much variance as possible for a given task, they are concurrently challenged to remain biologically plausible. Hence, there have been debates in the past decades on symbolic representations of entire concepts like words versus distributed representations by hidden units. For processing lower level information in the occipital cortex, there are single neurons that respond to a certain orientation of a feature (Hubel & Wiesel, 1962). Once this basic visual information is bound into a more complex concept however, the representation by one neuron would be inefficient and too vulnerable to lesions. Hence, neuroimaging data by Quian Quiroga et al. (2008, 2009) provided strong evidence that usually a group of neurons is activated in the higher order brain regions such as the MTG in response to a visually presented stimulus. Quian Quiroga and Kreiman (2010) further argued that even though some more unique representations can result into a very sparse neural coding, they still remain distributed. Moreover, a selective response by one neuron to a single concept does not allow the conclusion that this particular neuron conforms to the entire representation of that concept, but is more likely a distinct part of an activation pattern. When looking at the biological plausibility from this perspective, IAMs with their localist approach seem to not fare well relative to models with distributed representations.

A big advantage of localist multilayer models is that they offer the opportunity to illustrate every processing step in the brain transparently, without “hiding” information as apparent for models with distributed representations. The AROM consists of four layers, from low-level representations of single visual features and letters to high-level orthographic and semantic processing (**Fig. 2**; Hofmann et al., 2011; Hofmann & Jacobs, 2014). The changes of activation in every layer for every node can be investigated conveniently at every processing step. In the case of simulating semantic influences during priming, the semantic layer interacts with the orthographic layer to modulate the recognition speed of the target word. The activation in the semantic layer is based on co-occurrence statistics, which allow direct conclusions from the model data to the behavioral data of STUDY A (see section 4.5) and the brain data of STUDY B. Regarding STUDY B, the results finally provided empirical evidence for the architecture of the model. This section further examines the implications of these findings, and how they might help to improve the model.

STUDY B followed the proposal by Hofmann and Jacobs (2014) to relate higher order brain connectivity during semantic processing to the semantic layer of the AROM (**Fig. 4**). They named the MTG and the LIFG as main representatives of the semantic layer to account for semantic retrieval and the resolution of semantic conflicts, respectively (c.f. Bedny et al., 2008). Concerning the LIFG region, a re-analysis of previously published data showed that direct associations computed by co-occurrences can predict LIFG activation: A strong direct association resulted in less neural activation in the LIFG (Hofmann &

Jacobs, 2014). Of note, semantic similarity quantified by the number of common direct associates was neither investigated nor controlled for at this stage of research. The findings in STUDY B suggest that mainly differences in the semantic relationship between two words (and not their direct association) influence LIFG activation. This assumption probably better captures the function of the LIFG to suppress irrelevant semantic information, which is even more critical when strategic processes like semantic matching require many cognitive resources (McNamara, 2005; Neely, 1977). Hence the generally inhibitive effect of semantic priming on lexical decisions at a long SOA, while direct associations remain facilitative.

The MTG was considered by Hofmann and Jacobs (2014) as the second region conforming to the semantic layer. By binding information from different modalities into a single concept, the MTG enables the rapid access to semantic representations. In theory, both, the LIFG and the MTG, should share a strong functional connection. If a target word is pre-activated by a related prime, semantic information about the target can be acquired quickly. Thus, LIFG and MTG activation is minimized. On the other hand, if pre-activated words have to be suppressed due to an unexpected target word, neural responses in both regions should increase to quickly obtain the semantic information of the target and to resolve any semantic conflicts. Looking at STUDY B, it seems that the LIFG played a more central role for primed lexical decisions, as MTG effects were revealed only after using an uncorrected $p < 0.001$. Moreover, no significant connectivity in the PPI analysis could be observed between the two areas. Next to the explanation of an insensitivity of fMRI to temporal regions (cf. Sachs et al., 2011; Tivarus et al., 2006), it might be that the paradigm was not suited to reveal strong responses in the MTG. The priming task, as conducted in the present thesis, required an implicit processing of semantics, while participants had to focus on the decision whether a word or nonword was displayed. By changing the task slightly to decide between an animal word and no animal word, Weber et al. (2016) found highly significant effects in the MTG also for fMRI. Due to the available semantic information about the stimuli, general features of animals could be retrieved by the participants already at the beginning of the task. This probably allowed a stronger involvement of the temporal cortex into the decision making process. Another indication for this assumption is the observation from Bedny et al. (2008), revealing that the MTG is functionally separable from the LIFG when repeating the same (e.g. about animals) semantic information.

The PPI analysis in STUDY B further suggests that the LIFG directly communicated with the fusiform gyrus but not with the occipital cortex during the resolution of semantic competition. The fusiform gyrus most likely acted as interface of sublexical to lexical information between the occipital cortex and the LIFG, outlining the ventral visual pathway (Cohen et al., 2000; Mishkin et al., 1983). This route usually includes the MTG to receive input from the fusiform gyrus. Whether the temporal areas were skipped (i.e. of less importance for this task) or not detectable by fMRI cannot be fully resolved based on the present data (see above). No direct connection between the semantic network and the occipital cortex, but linked via an integral system like the fusiform area, is in accordance with the layered structure of the AROM, however.

Importantly, PPIs do not allow conclusions about the direction of the functional dependency. The AROM suggests a bidirectional excitatory connection between the orthographic and semantic layer (see **Fig. 2**). This setup addresses facilitation of the target identification via pre-activation by the prime word. Inhibition of the target word can occur if other strong associates of the prime become activated to compete with the target. While neurons cannot fire bidirectionally, the basic principle should be similar in the brain: When semantic competition emerges, top-down feedback is required for further evaluation. This feedback might even reach occipital regions (= the feature layer) e.g. to delay new visual input or to prepare an eye movement (for further discussion on this topic, see section 4.8).

While the main function of the hippocampal area concerns episodic memory (e.g. Marr et al., 1991; O'Reilly et al., 2014; Yassa & Stark, 2011), there have been reports of essential contributions also during semantic processing (e.g. Binder et al., 2009; Nobre & McCarthy, 1995; Ranganath & Ritchey, 2012). The hippocampus is anatomically very close to the fusiform gyrus, which share neural connections via the parahippocampus. In addition, the MTG is linked to the perirhinal cortex, a subregion of the hippocampus (**Fig. 18**; Dalton & Maguire, 2017; O'Reilly et al., 2014). Ranganath and Ritcheys (2012) review collected numerous neuroimaging studies, in which the hippocampus showed distinct responses to semantic priming and semantic discrimination. In one of these studies, Nobre and McCarthy (1995) reported a dependence of MTG activation on the hippocampus during priming. Hence, the ability of the hippocampus to generalize and to emphasize a common feature of two stimuli might provide critical support also to the LIFG for disentangling semantic conflicts.

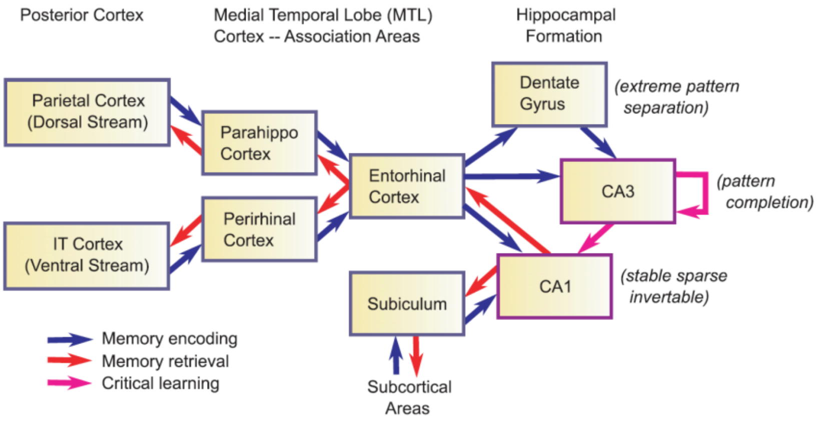


Fig. 18: *The hippocampal system and the functional connectivity of its subregions as proposed by O'Reilly et al. (2014). The dentate gyrus is responsible for the detection of a distinct pattern from a stimulus or an event. The CA3 includes a recurrent wiring to generalize across objects.*

Section 4.5 proposed a recurrent mechanism for the AROM to maintain semantic activation when no stimulus is presented, like the blank phase between the prime and target word. Models of the hippocampal system suggest such a loop in the CA3 region to reactivate associations until they are needed for retrieval by the semantic network (**Fig. 18**; O'Reilly et al., 2014). Therefore, a subroutine was coded into the AROM to account for this recurrent process. During the last cycle of the prime presentation, the current semantic activation was stored for every node. With the beginning of the blank phase, this activation was submitted to the input of the semantic layer at every cycle until the target onset. Furthermore, a parameter was added for the stored activation to slowly decline at longer SOAs, which should complement the biological process of decaying short-term information. This decay parameter was set to 0.03. Thus, after seventeen cycles of blank phase (= the long SOA of 1,000 ms), the semantic activation exerted by the prime was almost half as effective. Due to the backward connection from the semantic layer to the orthographic layer, influences by recurrent semantics on the subordinated layers were allowed while no stimulus was presented.

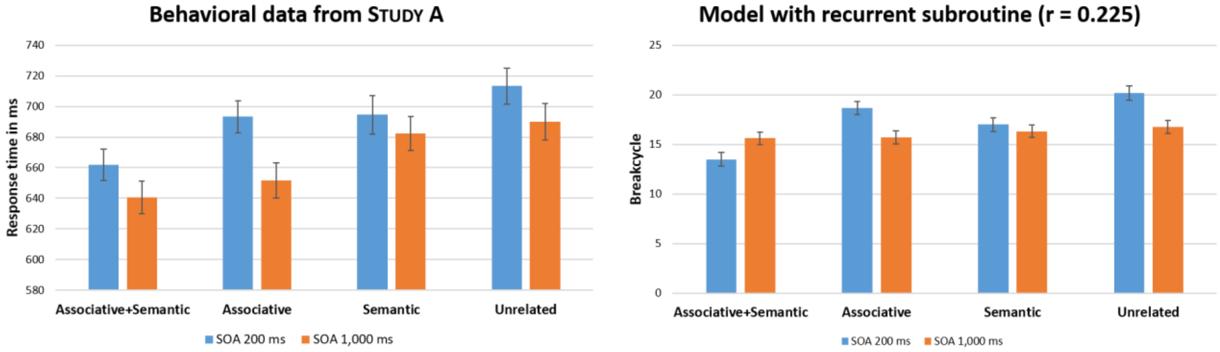


Fig. 19: *Mean response times per condition from Study A (left) in comparison with the mean breakcycles from the model data with a recurrent subroutine (right). The error bars reflect standard errors.*

As indicated in **Fig. 19**, the AROM was able to account for the SOA effect in a biologically plausible way with the support from a recurrent subroutine, and thus provided a better fit to the behavioral data (with recurrence: $r = 0.225$; no recurrence: $r = 0.190$; cf. **Fig. 14**). By increasing the excitation parameter α from the semantic layer to the orthographic layer from 0.12 to 0.15 (see section 4.5 for an overview on the parameter settings), even more variance could be explained ($r = 0.2885$). The general pattern across conditions remained identical between the two models (fully inherited parameters versus increased excitation from semantics to orthographics), but with stronger effect sizes in the latter one. For reasons of redundancy, the following analysis concentrates on the model with fully inherited parameters, which is highlighted in **Fig. 19** (right).

A 2 (Direct association: Strong/No) × 2 (Semantic similarity: High/No) × 2 (SOA: Short/Long) by-items ANOVA with breakcycle as dependent variable revealed main effects for direct association ($F_2(1, 180)$

= 12.90, $p < 0.001$, $\eta_p^2 = 0.069$; Strong: 15.88 cycles, No: 17.56 cycles), semantic similarity ($F_2(1, 180) = 22.43$, $p < 0.001$, $\eta_p^2 = 0.115$; High: 15.61 cycles, No: 17.83 cycles) and SOA ($F_2(1, 180) = 6.98$, $p < 0.01$, $\eta_p^2 = 0.039$; Short: 17.34 cycles, Long: 16.10 cycles). Furthermore, semantic similarity interacted significantly with SOA ($F_2(1, 180) = 17.53$, $p < 0.001$, $\eta_p^2 = 0.092$). Significant differences in breakcycles by the semantic relation was observed at the short SOA ($t(180) = 6.08$, $p < 0.001$), but not at the long SOA ($t(180) = 0.40$, $p = 0.687$). Direct association and SOA interacted slightly but insignificantly ($F_2(1, 180) = 3.01$, $p = 0.084$, $\eta_p^2 = 0.017$). *T*-tests showed that a strong direct association reduced the breakcycles at the short SOA only (short: $t(180) = 3.63$, $p < 0.001$; long: $t(180) = 1.36$, $p = 0.174$).

In comparison to the original model without a recurrent subroutine (cf. **Fig. 14**), these results suggest an improvement of the model data in several ways. Most obviously, the SOA effect was reverted to a faster target identification at a long SOA. While delivering a similar pattern as presenting the prime for the full duration of the SOA to the model (cf. **Fig. 15**), the revised version holds the premise of biological plausibility and a correct reflection of the procedure in STUDY A and B. In addition, the model was now able to correctly identify almost all target words also at the long SOA (> 95% correct). The high error rates for the models without a blank phase (only 5 – 25% correct recognitions at the long SOA; see **Fig. 15**) were likely related to an “over-activation” of the prime and its (mainly) orthographic and (some) semantic neighbors at the long SOA. Hence, a lot of the wrong identifications had many letters in common with the prime. Showing a prime for twenty cycles must have evoked a strong co-activation of those words, which suppressed the target word entirely. As the recurrent subroutine exerted an influence mainly on the semantic layer, orthographic neighbors of the prime remained comparably silent.

Another improvement concerns the interaction of the factors. On the one hand, direct association and semantic similarity no longer interacted with each other, which supports the finding of their dissociability (see STUDY A). Then, a high semantic similarity facilitated the target recognition at the short SOA only, which is also identical to the empirical data. Opposite to the general observations in the priming literature however, no priming effect occurred in the model data by direct associations at the long SOA (cf. **Fig. 19** right). It appears that the model currently overvalues semantic relations and their potential conflicts, which suppress the effect by direct associations at longer SOAs. Future attempts to resolve this issue might be successful by further tuning the excitatory and inhibitory parameters of the orthographic and the semantic layer.

Overall, the brain data from STUDY B provided requisite information about the functional connectivity of the semantic network during primed lexical decisions for the implementation of a recurrent subroutine in the AROM. This allowed the model to maintain semantic information between the presentation of the prime and target word, thus portraying the function of the CA3 region of the hippocampus.

4.7 EXTENDING THE AROM BY A CONJUNCTIVE LAYER

Next to priming studies, the AROM was utilized to predict recognition memories on studied versus new items (Hofmann et al., 2011). Hofmann et al. (2011) further manipulated the associative cohesion (High/Low) of the stimuli. This improved the recollection of studied words with a high cohesion, and evoked more false memories for new words with many direct associations to the studied words. The behavioral data was successfully explained by the mean semantic activation of the words in the first seven cycles (also see Jacobs et al., 2003 for the methodology). The effect of "studied words" was implemented in the AROM by increasing their initial semantic activation. Hence, recollection from memory was rendered rather artificially as it should occur in the MTG. The source of critical learning, the hippocampus, was not depicted by the model, however.

A more specific involvement of the hippocampus during learning of semantic and episodic information was postulated in the complementary learning systems (CLS) theory by McClelland et al. (1995). This framework suggests a neocortical and a hippocampal learning system. The hippocampus is responsible for quick learning, while the neocortex stores generalizable information. As recognition memory tasks require rapid semantic encoding and retrieval, a high demand is put on the hippocampus (Stark & Squire, 2000). Lesion studies revealed that the dentate gyrus is critical for emphasizing unique features (pattern separation) not only during encoding, but also during memory retrieval to increase its precision (Hainmueller & Bartos, 2020). In the CA3 subregion, slightly distinct input patterns can be activated repeatedly to form a common pattern for retrieval (pattern completion; e.g. O'Reilly et al., 2014; Yassa & Stark, 2011).

This section focusses on the function of the dentate gyrus, which codes item information into very sparse neural activations. Therefore, a unique neural pattern can represent a concept without interfering with other memories (O'Reilly et al., 2014). Kumaran and McClelland (2012) implemented this principle into an IAM called REMERGE, which forms pattern separated hippocampal representations in a conjunctive layer. As the name implies, the conjunctive layer was utilized to store the critical dependency of two concepts (e.g. A and B). They showed that the model was able to predict the encoding process of transitive inferences (if A > B and B > C, then A > C) and paired associative inferences (if AB and BC belong together, then AC belong together), for example. Kumaran and McClelland (2012) further tested their model in a recognition memory paradigm. It performed similarly well with and without the conjunctive layer, which suggests that the hippocampal implementation neither had a cost nor any benefit for the recognition. It might be possible however, that a model with a full implementation of semantic long-term memory, such as the AROM, could profit from a hippocampal system to predict recognition memory.

On that basis, the present thesis introduces an extension of the AROM by a conjunctive layer (further called c-AROM) to simulate the retrieval of studied versus unstudied words with a high or low semantic overlap to each other. In the first step, the model collects data about the distinct semantic features of a stimulus by scanning the semantic layer for unshared direct associations. Then, the conjunctive layer forms nodes equal to the number of distinct features, each representing the conjunction of the stimulus and the particular feature. If no distinct features exist, no conjunctive layer is created. The conjunctive units are wired with the stimulus and the feature representations in the semantic layer to send and receive activation (see **Fig. 20** for an overview).

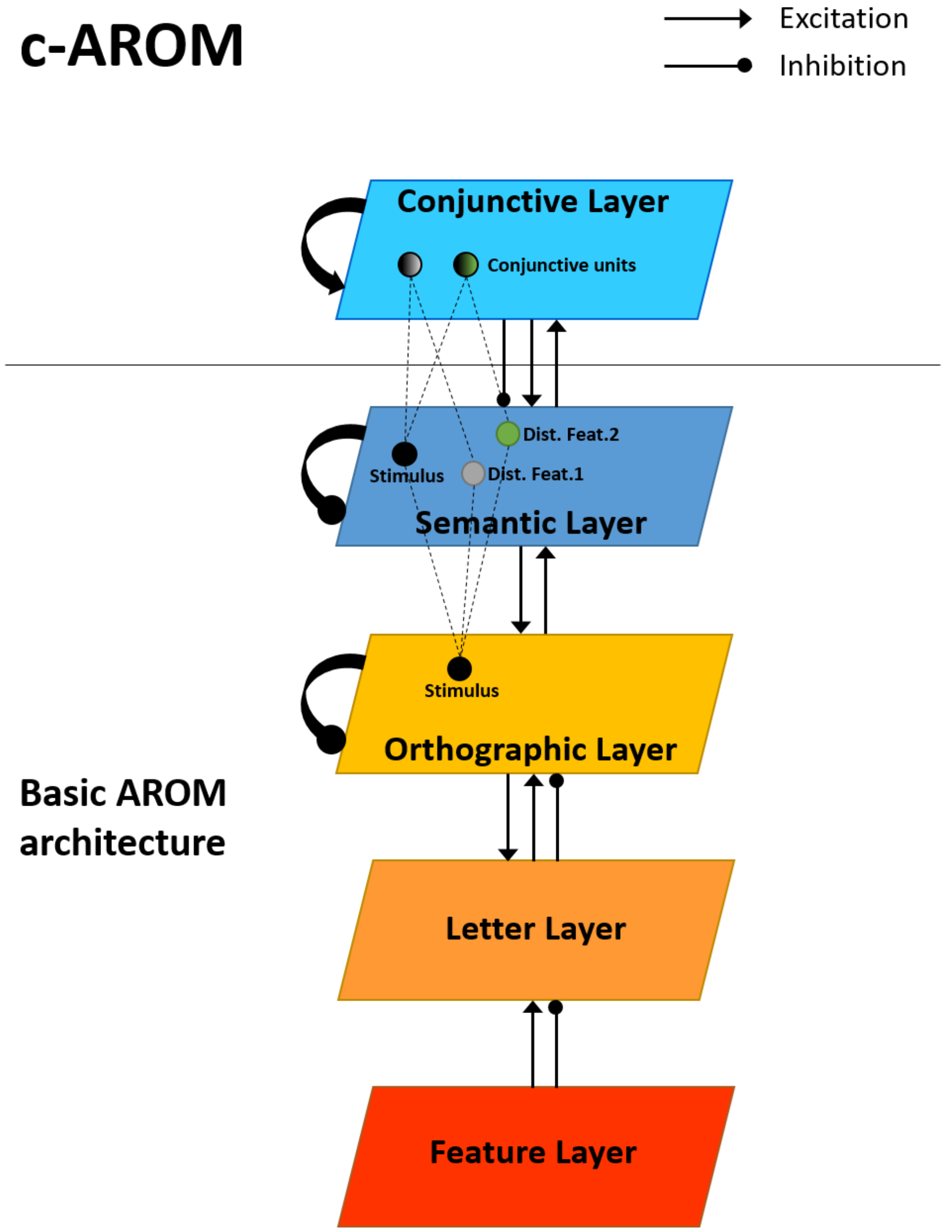


Fig. 20: *Schematic depiction of the AROM (Hofmann et al., 2011; Hofmann & Jacobs, 2014) with a conjunctive layer (c-AROM). In the conjunctive layer, the stimulus and its distinct features form respective conjunctive units, similar to the pattern separation process in the dentate gyrus. This allows the model to account for striking semantic details about a stimulus.*

In the following simulation, the linked nodes in the semantic layer were allowed to excite the conjunctive units by α = 0.1, as stimulus presentation should activate the respective neurons in the Hippocampus for retrieval. It was further assumed that conjunctive units are crucial for the dissociation of words with a high semantic overlap, while they are not as essential for less overlapping stimuli. In other words, less distinct features should exist at a high semantic overlap relative to a low overlap (cf. **Table 14**), making them more critical for a successful recognition. Hence, an adaptive function was implemented to induce excitation from the conjunctive units to the stimulus representation in the semantic layer when only a few distinct features existed. If a stimulus had many distinct features, the influence by conjunctive units was slightly inhibitive to illustrate a costly cognitive process without much gain of information. Therefore, the exerted activation of one conjunctive unit to the stimulus representation in the semantic layer ($Act_{c_{ij} \to s_i}$) was calculated by its own excitatory effect of $\alpha_{c_{ij}}$= 0.2 minus the inhibitive effect of $\gamma_{c_{ix}}$= 0.03 times the number of other distinct features (see Equation(1)). Moreover, the conjunctive units started at a slightly positive resting value of 0.1 and could excite themselves by α = 0.2 at every cycle of memory recollection, which made them more salient in comparison to other direct associates of the stimulus.

$$Act_{c_{ij} \to s_i} = \alpha_{c_{ij}} - \sum_{x=1}^{n} \gamma_{c_{ix}}$$

Equation(1)

Empirical data was collected from thirty-six native German speaking participants (25 female, *M* = 24.83 years, *SD* = 5.33 years), who were asked to learn 100 visually presented German words and to later recognize them among 100 newly shown words. Every stimulus was displayed for 3,000 ms during the study and the recognition phase. The stimuli were manipulated by their semantic cohesion (High/Low), and were carefully matched on the psycholinguistic variables of associative cohesion, word frequency, word length and number of orthographic neighbors (all *F*'s < 1; **Table 14**). Four participants were excluded from the analyses because of high error rates (> 40%).

Table 14: *Mean values (standard deviation in parentheses) of the controlled variables of the utilized stimulus set. The values of Semantic Overlap (=semantic cohesion) were acquired by counting the total number of common associates between a stimulus and all other stimuli. The values of Num. DAs refer to the associative cohesion of the stimuli.*

Condition	Semantic Overlap	Distinct Features	Num. DAs	Word length	Freq. Class	Orth. Neighb.
Old – High Sem. Overlap	6049.34 (760.30)	3.54 (3.48)	19.12 (6.33)	6.44 (1.42)	9.88 (1.56)	1.30 (2.63)
Old – Low Sem. Overlap	4291.60 (603.34)	6.06 (5.61)	19.34 (7.10)	5.58 (1.36)	10.16 (0.98)	2.52 (3.18)
New – High Sem. Overlap	6097.54 (650.65)	3.82 (4.34)	21.28 (8.60)	5.58 (1.50)	10.06 (1.52)	1.84 (2.15)
New – Low Sem. Overlap	4254.18 (651.18)	7.84 (7.02)	18.86 (9.70)	6.18 (1.37)	9.74 (1.03)	1.30 (2.02)

A 2 (Oldness: Old/New) × 2 (Semantic overlap: High/Low) by-subjects ANOVA with error rate as dependent variable revealed a significant oldness main effect ($F_1(1, 31) = 40.51$, $p < 0.001$, $\eta_p^2 = 0.566$; Old: 66.9% correct, New: 81% correct), which is related to the general tendency of subjects to press "new" when unsure. Furthermore, oldness interacted significantly with semantic overlap ($F_1(1, 31) = 14.06$, $p < 0.001$, $\eta_p^2 = 0.312$). For studied words, a high semantic overlap resulted in more correct responses ($t(1, 32) = 2.37$, $p < 0.05$; High: 68.8% correct, Low: 64.9% correct). A false memory effect occurred for newly presented words which were semantically close ($t(1, 32) = -3.40$, $p < 0.01$; High: 78.1% correct, Low: 83.8% correct; **Fig. 21** left).

As the behavioral data showed the expected results, the same stimuli and procedure were used for the simulations. The semantic activation of the stimulus after reaching the breakpoint, and thus the likeliness that this word could be recollected from memory, functioned as predictor for the number of correct responses. Semantic activation (in the model) and the number of correct responses (in the behavioral data) were expected to correlate positively for studied stimuli with a high semantic overlap (recollection), but negatively for new stimuli with a high overlap (false memories). Therefore, the correlation analysis of the model data and the empirical data was performed for every condition separately to capture the predictive power of the c-AROM in these diverging cognitive circumstances.

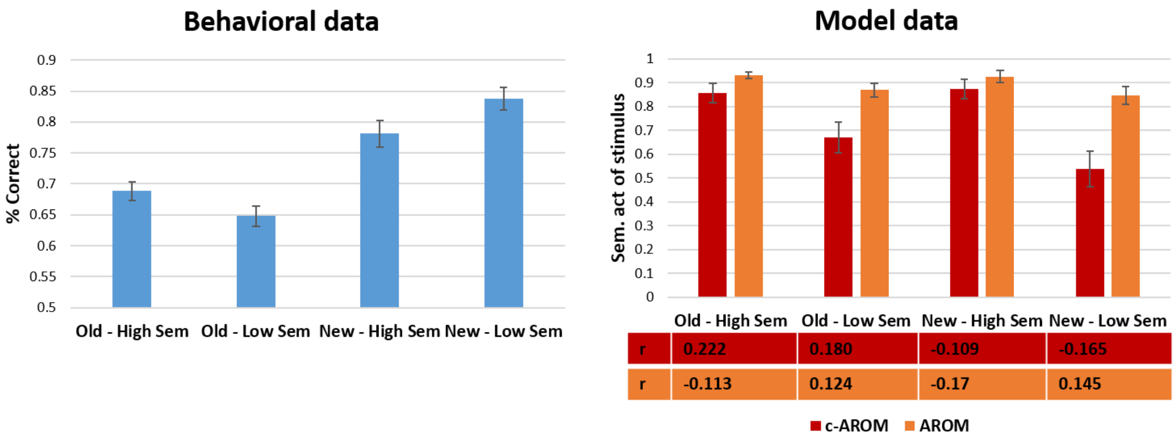


Fig. 21: *Mean percentage of correct responses per condition in the empirical study (left) compared with the mean semantic activation of the stimulus in the AROM and c-AROM (right). The correlation values on the right refer to the respective condition of the behavioral data. The error bars reflect standard errors.*

The c-AROM successfully predicted that a higher semantic activation for studied words with a strong semantic overlap leads to more correct memories (r = 0.222). The rate of correct responses to studied words with a low semantic overlap could also be explained sufficiently (r = 0.180). In addition, an increased semantic activation for new words with a high semantic overlap suggests more false memories (r = -0.109), while less overlapping newly presented words can often be recognized correctly (r = -0.165; see **Fig. 21**). The benefits of the conjunctive layer become more evident when comparing the results to simulations by a default AROM. The AROM predicts less correct responses for old words with a high semantic cohesion (r = -0.113), which is opposite to common findings. Similarly, the positive correlation for new words with a low semantic overlap to a correct memory (r = 0.145) is inverted to the c-AROM and the general consensus (**Fig. 21** right).

While still being in a proof-of-concept phase, this first attempt for the inclusion of a conjunctive layer to model the recognition memory process seems promising. Of course, the model was not opted to account for the decision criterion by participants to decide for new stimuli more often, which inflates the rate of correct responses in the corresponding conditions. Other than that, the c-AROM allows a good fit to the empirical data based on a biologically plausible concept: pattern separation by the dentate gyrus. When asked to learn PENGUIN among a number of bird species, its encoding will profit from the distinct features of not being able to fly or being an enduring diver. Such few but striking differences will improve the recognition of PENGUIN dramatically. If one has to remember LAWNMOWER among many bird species, the large number of distinct semantic features should be less important for a successful recognition. Here, CA3 activation (and thus pattern completion) should be more critical for recollecting the word. Further support for this suggestion needs to be acquired in the future, e.g. by conducting a high resolution neuroimaging study with a focus on the neural responses in the hippocampal subregions CA3 and dentate gyrus.

4.8 MULTIPLE PRIMING AND LAG PRIMING

In most studies, primed lexical decisions are based on one prime followed directly by a related target word (cf. STUDY A and STUDY B). It has been shown that priming the target with two related words (e.g. COPPER and BRONZE priming METAL) can result in an additional boost of the priming effect (further referred to as "multiple priming"; Balota & Paul, 1996; also see McNamara, 1992). Moreover, Balota and Paul (1996) reported that the priming effect of a directly preceding associated prime was stronger than if an intervening unrelated stimulus was presented (further referred to as "lag priming"). While a lag of one often still results in significant priming, two intervening unrelated words can already nullify the effect (McNamara, 1992, 2005). In relation to the spreading activation theory (Collins & Loftus, 1975; Quillian, 1967), this suggests that priming is a very short-lived process, which decays quickly but remains strong enough for a lag of one unrelated stimulus. Joordens and Becker (1997) were able to find priming effects at larger lags of up to eight intervening stimuli, e.g. by placing a number of difficult nonwords (e.g. pseudohomophones) between the prime and target, or by studying the targets pre-experimentally. Critically however, more recent studies failed to replicate these observations, questioning those previously observed "long-term" lag effects (cf. McNamara, 2005; Zeelenberg & Pecher, 2002).

The aim of the following Experiments I - III was to investigate multiple priming and lag priming when using co-occurrence based associations. Lag priming over more than one intervening stimulus seems unlikely when looking at the more recent literature (McNamara, 2005; Zeelenberg & Pecher, 2002). Moreover, long-term lag effects would contradict with the spreading activation theory, as activation decays at a rapid rate when a prime stimulus is no longer presented (McNamara, 2005). To the best knowledge of the author, a significant increase of priming by more than two primes in succession has not been reported yet, either. Hence, it would be of relevance for future studies to see at which point the priming effect reaches its ceiling in the case of multiple priming, and what (if observable) more distant lag effects would implicate for models based on the spreading activation theory such as the AROM.

The Experiments consisted of a fixed sequence of stimuli (Experiment I and II: 200 noun words and 200 nonwords; Experiment III: 224 noun words and 224 nonwords). Co-occurrence statistics were extracted from the *deNEWS* corpus (version 2011) of the Leipzig Wortschatz Project, which contains 70 million sentences and 1.1 billion words (Goldhahn et al., 2012). As the error rates were generally too low (~5% on average), response times were the primary dependent variable of interest. Continuous predictors were used to explain the response time on the words. Thus, the analyses relied on item-based stepwise (forward) linear regressions with the Akaike information criterion (AIC) as estimator for the inclusion of a predictor. The data on the nonwords was excluded prior to the analyses, as well as responses that were shorter or larger than three times the standard deviation of the mean response time per participant. Furthermore, the threshold for inclusion of a participant was set to 80% or more correct responses.

Experiment I functioned as a pilot to investigate lag effects from zero to four intervening unrelated words or nonwords. The word stimuli were divided into pairs of related words and an identical total number of unrelated words. One half of the related word stimuli were directly associated and the other half semantically related. The related word pairs were equally often intervened by zero to four nonwords and / or unrelated words. For instance, when a directly associated word pair was intervened by two stimuli (= lag of two), the target N was primed by N-3, while N-1, N-2, N-4 and N-5 were all unrelated to N. Correlations between word frequency, orthographic neighbors and word length were kept at $r < 0.3$ to reduce the multicollinearity. Half of the nonwords were random letter strings, while the other half followed the phonological rules of German language. A trial started with the visual presentation of a fixation cross (+) for 500 ms. Then, a stimulus was presented for 1 sec in uppercase. During that time, the participants had to respond with “word” or “nonword” by pressing the corresponding button. Hence, a response was required for every stimulus, contrary to classic primed lexical decisions, in which the prime has to be processed but not responded to. Thirty native German speakers (19 female, M = 28.73 years, SD = 11.59 years) participated in the study. None of the participants were excluded because of error rate. The predictors of the regression model were word frequency, word length, orthographic neighbors, the direct association at a lag from zero (N primed by N-1) to four (N primed by N-5; all lags in separate predictors), and the semantic similarity at a lag from zero to four (all lags in separate predictors).

At r_{adj}^2 = 0.305, the regression model was able to explain the response times significantly ($F(1,195)$ = 87.10, $p < 0.001$). The only significant predictor added to the model was word frequency (**Table 15**): Faster responses were made for high frequency words, which is a standard observation in the word recognition literature (e.g. Inhoff & Rayner, 1986). All other predictors were excluded by the regression model.

Table 15: *Prediction of response times from Experiment I by stepwise linear regression (forward) with AIC as estimator for the inclusion of a predictor, and linear regression including all predictors. Significant predictors (p < 0.05) are highlighted in bold. DA = direct association; Sem. = semantic similarity.*

	β	*SE* β	*t*	*p*
Stepwise regression - forward (AIC = 1,412.34; r^2_{adj} = 0.305)				
(Constant)	559.37	4.45	125.69	**< 0.001**
Word frequency	-11.17	1.20	-9.33	**< 0.001**
Linear regression (r^2_{adj} = 0.315)				
(Constant)	448.13	10.72	41.81	**< 0.001**
Word frequency	-7.51	0.92	-8.15	**< 0.001**
Word length	0.03	2.33	0.02	0.988
Orthographic neighbors	-1.69	1.08	-1.56	0.119
DA lag 0	2.24	5.16	0.43	0.665
DA lag 1	-4.79	4.93	-0.97	0.333
DA lag 2	-0.24	6.16	-0.04	0.969
DA lag 3	-1.78	6.89	-0.26	0.797
DA lag 4	-4.16	7.89	-0.53	0.598
Sem. lag 0	-0.22	0.66	-0.34	0.733
Sem. lag 1	1.06	0.65	1.63	0.106
Sem. lag 2	0.33	0.81	0.40	0.688
Sem. lag 3	-0.07	0.75	-0.10	0.923
Sem. lag 4	0.12	1.38	0.09	0.931

A linear regression with all predictors (*F*(13,195) = 7.17, *p* < 0.001) further indicated a small insignificant influence of the semantic similarity at a lag of one intervening unrelated stimulus (**Table 15**). As the spread of activation takes some time to reach the indirect connections of semantically similar words, such a slightly delayed effect would be in line with the theories behind the co-occurrence approach. In addition, the model predicted a longer response time at a higher semantic similarity, which would conform to default observations for strategic priming, e.g. as reported in STUDY A.

The failure to find any solid evidence for lag priming (or even immediate priming at a lag of zero) was probably caused by the fact that a comparably large number of the 200 data points per predictor was filled with zero values when a word was not related to the preceding stimuli. Hence, the regression model was unable to fit the data. Relatedly, the lag three and four predictors were strongly correlated (*r*'s > 0.7) because of the high number of zero values (the lag of zero, one and two predictors showed only uncritical correlations of *r* < 0.3). This issue should be addressable by reducing the investigation to lags from zero to two, which increases the number of data points per predictor to also provide less correlated data.

Further justification for the removal of more distant lag effects is given by recent research, which indicates that such effects are highly unstable, and probably rely on episodic components (e.g. a pre-experimental study phase) to be observable at all (McNamara, 2005). McNamara (2005) also pointed out that the absence of long-term lag effects provides support for spreading activation models due to the assumption of a fast decay rate of activation. Therefore, a zero finding on long-term lag effects would suit the present work. Final conclusions on lag effects will be made in Experiment III, while the following Experiment II concentrates on multiple priming.

Experiment II looked at multiple priming by up to six related words in succession (= one block). The words in one block were selected to be semantically related with each other. For reasons of simplicity, direct associations were not regarded in this pilot study. In total, the stimulus sequence contained nine blocks of six related words, nine blocks of five related words, eleven blocks of four related words, ten blocks of three related words, nine blocks of two related words, and nine blocks of just one word to reduce the expectancy of the following lexical decision. No critical correlations existed between word frequency, orthographic neighbors and word length (*r*'s < 0.3). The nonwords were identical to Experiment I, and were put into blocks of similar sizes as the words. The procedure remained the same as above, but with a fixation cross duration of 1 sec to allow more time for processing the stimuli. Thirty-seven native German speakers (33 female, *M* = 21.81 years, *SD* = 3.1 years) participated in the study. None of the participants were excluded because of error rate. The predictors of the regression model were word frequency, word length, orthographic neighbors, and the semantic similarity of the word N to either N-1, N-2, N-3, N-4 or N-5 (all in separate predictors).

At r^2_{adj} = 0.425, the regression model predicted the response times significantly (*F*(5,199) = 31.30, *p* < 0.001). The significant predictors consisted of (from strongest to weakest) the semantic similarity of N to N-1, orthographic neighbors, word frequency and the semantic similarity of N to N-2. Furthermore, the predictor semantic similarity of N to N-3 almost reached a significant influence on the response time, and was included by the regression model because of a better fit based on the AIC value (see **Table 16** for an overview). For all those predictors, a higher value reduced the response time.

Table 16: *Prediction of response times from Experiment II by stepwise linear regression (forward) with AIC as estimator for the inclusion of a predictor. Significant predictors ($p < 0.05$) are highlighted in bold. Sem. = semantic similarity.*

	β	*SE* β	*t*	*p*	r^2_{adj}	*Δr²*
Stepwise regression - forward (AIC = 1,482.70; r^2_{adj} = 0.425)						
(Constant)	524.92	18.00	29.16	**< 0.001**		
Sem. N to N-1	-1.99	0.33	-6.04	**< 0.001**	0.254	0.254
Orthographic neighbors	-6.04	1.46	-4.13	**< 0.001**	0.326	0.072
Word frequency	-4.82	1.46	-3.30	**< 0.001**	0.378	0.052
Sem. N to N-2	-1.05	0.39	-2.71	**< 0.01**	0.407	0.030
Sem. N to N-3	-0.77	0.41	-1.86	0.064	0.425	0.018

In line with Balota and Paul (1996), the two preceding semantically related words positively influenced the response time of the next word. In addition, the regression analysis indicated a small effect of the third last stimulus on the presented target word. **Fig. 22** shows that the response time decreased with diminishing effectiveness for up to five semantically similar words in succession, while the sixth word had the tendency to increase the response time, again. This increase after many succeeding word stimuli was probably caused by a shift of expectation towards a nonword response (Wagenmakers et al., 2008).

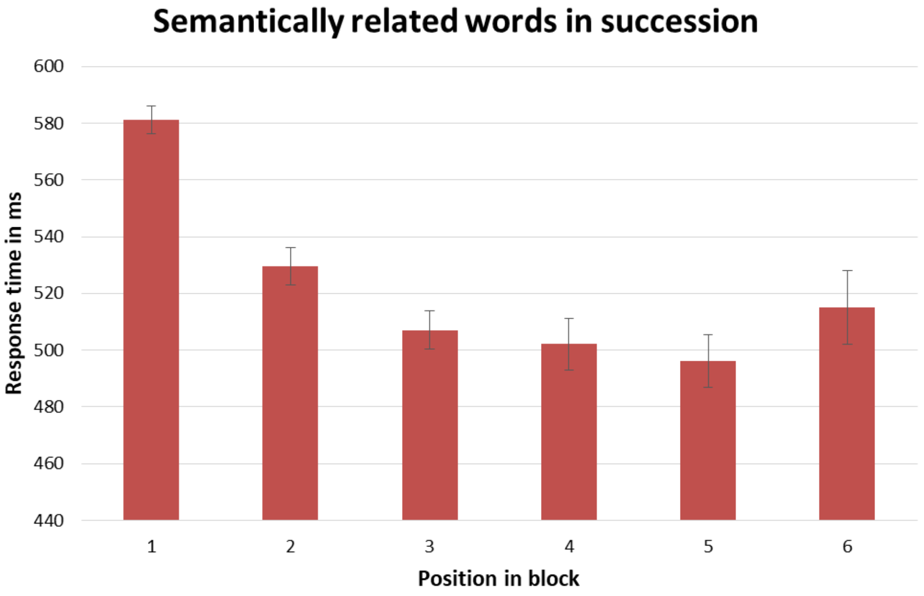


Fig. 22: *Mean response times for the first to sixth semantically related word in succession. The first word was preceded by unrelated stimuli, while the successive words of a block were primed by the previous. For instance, the word N at position 4 was primed by N-1 (= position 3), N-2 (= position 2) and N-3 (= position 1), but not by N-4 and N-5 as they were unrelated stimuli. The error bars reflect standard errors.*

While it seems that up to three words can prime the succeeding word, the interpretation of these findings is hindered by the same reason as in Experiment I. There were many data points without semantic relations between the word N and N-4, or N-5. For instance, fifty-six (of 199 possible) semantic relations existed between N and N-1, while only nine relations existed between N and N-5 (as there were only nine blocks with six succeeding word stimuli). As consequence, the predictors of the semantic relation were correlated to a critical level (*r*'s > 0.3). Especially the slight influence by semantics from N-3 to N can therefore be interpreted with caution, only. Because of repeating issues with more distant effects, Experiment III was restricted to four succeeding relations.

Experiment III aimed to address the methodological issues of the previous two pilot studies, and investigated multiple priming as well as lag priming by direct associations and semantic relations. To increase the statistical power, 224 (instead of 200) word and nonword stimuli, respectively, were added to the sequence. Furthermore, not only the correlation of word frequency, orthographic neighbors and word length remained lower than *r* = 0.3, but also of all the predictors about the relationship. The nonword creation followed the same rules as above.

Multiple priming was limited to a succession of not more than four related words. One block of four stimuli could contain two to four related words in succession, while the remainder of a block was filled with nonwords. The relation between the words was matched on direct association and semantic similarity. In addition, two words could either be directly associated and semantically similar, purely directly associated or purely semantically similar, which was further balanced across all blocks. In total, forty of those blocks were created.

Lag priming was also limited to a maximum of two intervening unrelated words and / or nonwords (in any combination). Here, thirty blocks were created, each consisting of six stimuli with three words and three nonwords. Two of those words were either directly associated and semantically similar, purely directly associated or purely semantically similar, while the third word remained unrelated. The position of the two related words within the block was pseudorandomized and balanced across a lag of one and two intervening stimuli.

Furthermore, there were twenty-seven blocks, which contained one to four unrelated words and a number of nonwords to add up to four stimuli per block. The blocks of multiple priming, lag priming and the unrelated blocks were all pseudorandomized into a fixed sequence.

The procedure was identical to Experiment II. Forty native German speakers (31 female, *M* = 23.37 years, *SD* = 2.9 years) participated in the study. Five participants were excluded because of error rate. The predictors of the regression model were word frequency, word length, orthographic neighbors, the direct association of the word N to either N-1, N-2 or N-3 (all in separate predictors), and the semantic similarity of the word N to either N-1, N-2 or N-3 (all in separate predictors).

In the first stepwise regression model, all word stimuli from the multiple priming, the lag priming and the unrelated word blocks were included. At r^2_{adj} = 0.208, response times could be predicted by a significant regression model ($F(5,223) = 13.16$, $p < 0.001$). The included predictors were (from strongest to weakest) word frequency, the direct association of N to N-1, the semantic similarity of N to N-3 , word length and orthographic neighbors (**Table 17**). For all those predictors, except for word length, a higher value reduced the response time. In contrast, longer words increased the response time.

Table 17: *Prediction of response times from Experiment III by stepwise linear regression (forward) with AIC as estimator for the inclusion of a predictor. The first regression included the data from all word stimuli. The second regression contained words from multiple priming blocks only, while the third regression focused on lag priming blocks. Significant predictors (p < 0.05) are highlighted in bold. DA = direct association; Sem. = semantic similarity.*

	β	*SE* β	*t*	*p*	r^2_{adj}	*Δr²*
All word blocks Stepwise regression - forward (AIC = 1,628.45; r^2_{adj} = 0.208)						
(Constant)	545.05	21.81	24.99	**< 0.001**		
Word frequency	-6.84	1.40	-4.88	**< 0.001**	0.109	0.109
DA N to N-1	-10.90	3.75	-2.91	**< 0.01**	0.151	0.045
Sem. N to N-3	-1.86	0.67	-2.77	**< 0.01**	0.179	0.028
Word length	4.66	2.24	2.09	**< 0.05**	0.196	0.017
Orthographic neighbors	-2.79	1.44	-1.94	0.053	0.208	0.012
Multiple priming word blocks Stepwise regression - forward (AIC = 682.47; r^2_{adj} = 0.196)						
(Constant)	554.04	25.28	21.92	**< 0.001**		
Word frequency	-8.27	2.19	-3.78	**< 0.001**	0.113	0.113
Sem. N to N-3	-3.37	1.49	-2.27	**< 0.05**	0.158	0.045
DA N to N-1	-8.52	4.24	-2.01	**< 0.05**	0.186	0.028
Orthographic neighbors	-2.90	1.80	-1.61	0.112	0.196	0.010
Lag priming word blocks Stepwise regression - forward (AIC = 473.27; r^2_{adj} = 0.263)						
(Constant)	552.35	33.64	16.42	**< 0.001**		
Word frequency	-6.55	2.35	-2.79	**< 0.01**	0.100	0.100
Sem. N to N-3	-1.13	0.46	-2.46	**< 0.05**	0.172	0.072
DA N to N-2	-10.40	4.54	-2.29	**< 0.05**	0.195	0.023
Orthographic neighbors	-4.97	2.68	-1.86	0.068	0.232	0.037
Word length	5.36	3.18	1.68	0.097	0.263	0.031

When analyzing the blocks of multiple priming only, almost identical predictors were added to the significant model (r^2_{adj} = 0.196; *F*(4,92) = 7.01, *p* < 0.001), but in a different order: Word frequency, the semantic similarity of N to N-3 and the direct association of N to N-1 had a significant effect on the response time, while orthographic neighbors were included by the stepwise regression but stayed insignificant (**Table 17**). Again, a higher value of the predictors reduced the response time. In correspondence to the regression analysis, **Fig. 23** highlights the effects of priming by one to three successive words on the next word. Priming of the second word by the first word was largest if they were directly associated, hence the significant predictor in the regression analysis. Priming on the third word (thus N effectively primed by N-1 and N-2) did not occur when looking at the regression model, as also unrelated words in that position were recognized comparably fast (cf. **Fig. 23**). **Fig. 23** suggests, however, that two preceding words with a semantic relation evoked a marginal facilitative effect on the next word, even though the predictor was excluded by the regression model (β = -0.79, *SE* β = 0.74, *t*(224) = -1.07, *p* = 0.290; if added manually to the existing model). If a word was preceded by three semantically similar words, it was recognized significantly faster as indicated by the regression.

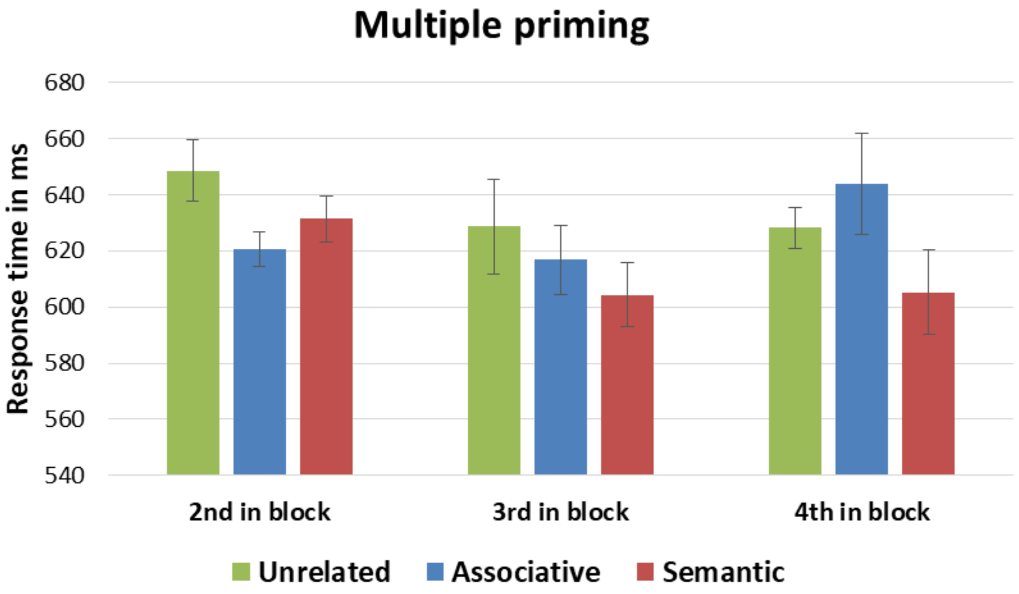


Fig. 23: *Mean response times of the second, third and fourth word in the multiple priming and the unrelated word blocks. If the second word was preceded by a directly associated word, the response time decreased. The third word in a block was not significantly influenced by direct association or semantics of the preceding words, while the last word was identified the fastest if the last three stimuli consisted of semantically similar words. The error bars reflect standard errors.*

Also the regression model of lag priming blocks successfully predicted response time data (*F*(5,66) = 5.74, $p < 0.001$). At $r^2_{adj} = 0.263$, word frequency, the semantic similarity of N to N-3 and the direct association of N to N-2 affected the response time significantly. Orthographic neighbors and word length were further added to the model, but remained slightly insignificant (**Table 17**). Again, a higher value in each of those predictors reduced the response time.

Fig. 24 presents the data on lag priming relative to the unrelated blocks. At a lag of one, a strong direct association facilitated the response of the target word (N primed by N-2). A high semantic similarity, on the other hand, influenced the target word recognition at a lag of two (N primed by N-3).

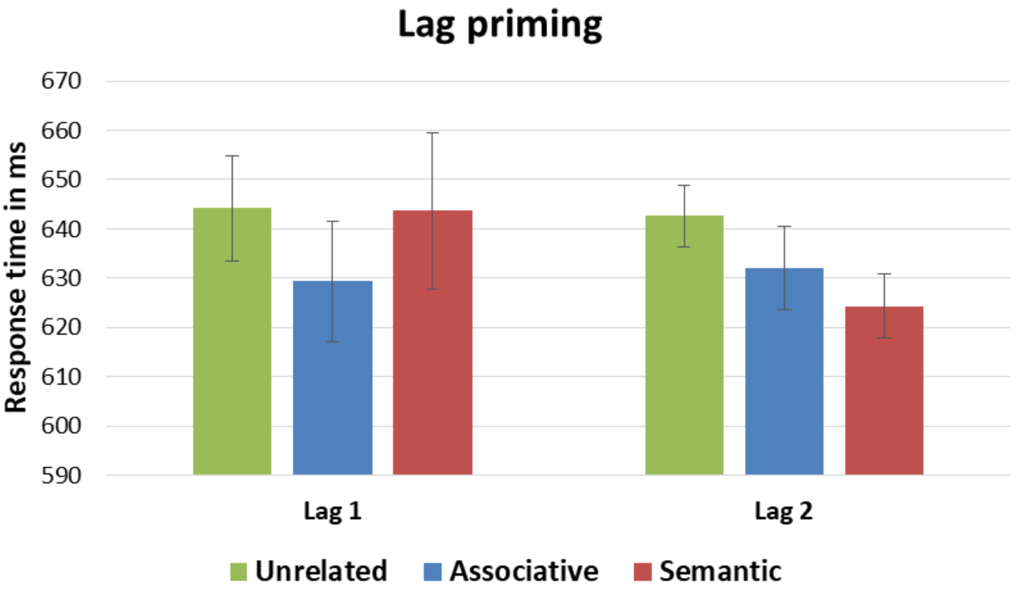


Fig. 24: *Mean response times at a lag of one or two intervening unrelated stimuli. Word identification was facilitated for directly associated words at a lag of one, and for semantically similar words at a lag of two. The error bars reflect standard errors.*

In general, the results of Experiment III suggest that priming by direct association occurred early and reached its limits fast, while it took longer for semantic similarity to exert an influence (of similar strength as direct association) on the target word. This temporal gap between direct association and semantic similarity seems explainable by the spreading activation theory, as direct associations reflect direct links in the network and thus can be accessed quickly in comparison to semantic relations, which rely on indirect connections. Furthermore, the SOAs in all experiments were long enough to evoke strategic processing, which facilitated direct associations and increased the semantic competition (McNamara, 2005; Neely, 1991). Hence, direct association could exert an immediate (multiple priming) or faster (lag priming) effect, while it took more cognitive resources to disentangle semantic conflicts (see STUDY A and B), resulting in a delayed availability of semantic information.

Regarding multiple priming, previous observations by Balota and Paul (1996) suggested that priming by two words can be stronger than if only one prime preceded the target word. Experiment II demonstrated that also a third prime in succession can affect the response time on the target, although some predictor variables were not under full experimental control. Experiment III took care of these methodological flaws and provided further evidence for an influence of the third last word on the currently presented target word. More precisely, the limit of how many primes can affect the response time of a target word appears to be dependent on the quality of the relation. The regression analysis indicates that a sequence of direct associations might reach their maximum of priming already after the first prime, when semantic effects just emerge (cf. **Fig. 23**). **Fig. 23** further suggests that responses on the third word were generally very quick, including unrelated words. Thus, the predictors from N to N-2 were unable to explain the behavioral data significantly. As pointed out by Wagenmakers et al. (2008), the speed of a response is connected to the criterion of the most probable response. Hence, two "word" responses in a row might have increased the likeliness to respond "word" also on the next stimulus, which could have resulted in a floor effect on the response time. After three "word" responses in a row, the response criterion was probably more balanced, again, to induce a late significant priming effect of semantic similarity. Next to the interpretation of a temporal difference between direct association and semantic similarity due to the spread of activation, one could also argue that these delayed effects of semantics were based on an accumulation of multiple stimuli of that type. In other words, one direct association could have primed as much as three semantic relations. However, this contradicts with similar findings for lag priming, where only one word primed the target.

Priming with a lag of one intervening stimulus was successfully reported and replicated in a few studies (e.g. Joordens & Becker, 1997; McNamara, 1992; Zeelenberg & Pecher, 2002). More distant priming occurred only under specific situations, which included episodic components or certain types of intervening stimuli, and still remained difficult to replicate more recently (Joordens & Becker, 1997; McNamara, 2005; Zeelenberg & Pecher, 2002). While the results of Experiment I did not provide a conclusive answer, Experiment III supports previous findings of lag one priming, and extends the scope to priming via a lag of two intervening stimuli. Target words were recognized significantly faster at a lag of one if the prime was directly associated, but not if they were semantically related. Semantically similar words required the duration of two intervening stimuli for significant priming, at which point direct association no longer influenced the target (see **Fig. 24**). This fosters the assumption of temporally diverging processes also when the prime was not immediately followed by the target. More distant lag effects might be possible on the basis of semantic relationships. However, Experiment I and II showed that it becomes exponentially more difficult to control for the psycholinguistic variables of last five (instead of just three) words on the current word.

4.9 THEORETICAL AND PRACTICAL IMPLICATIONS BY UTILIZING WORD CO-OCCURRENCES

The primary objective of STUDY A and B (including the affiliated research conducted in the sections 4.5 to 4.8) was to provide empirical support for the predictions of a neurocognitive model, the AROM, by using co-occurrence statistics. On that basis, the structure of the model could not only be tested on biological plausibility, but also extended in its function with the addition of a hippocampal framework. Next to this apparent benefit, there are further applications of using computationally determined word co-occurrences, not only in the psycholinguistic research, but also in other fields.

From a theoretical perspective, co-occurrences offer an opportunity for future research to clearly separate direct associations from semantic relations during stimulus selection (also see Rapp, 2002). In this light, also the classification of priming subtypes might become more defined. For instance, mediated priming (the indirect priming of e.g. LION by STRIPES via TIGER) was considered by Hutchison (2003) as a form of associative priming, even though the priming pattern does not match at long SOAs (also see section 4.3). McNamara (2005), on the other hand, considered mediated priming as a special type of priming with elusive priming effects. He discussed that indirectly connected words often contain some minor direct associative or semantic relation. This can sometimes result in successful indirect priming, while in other cases no difference to entirely unrelated word pairs is observable. Here, word co-occurrences might help to define what accounts for associative and semantic priming, respectively. In addition, they allow the illustration of associative and semantic priming by a single principle, without confounding factors like the subjective classification of word relationships by humans. Once set up, scripts for the extraction of co-occurrence data further provide a universal tool, which can easily be transferred into any language.

When performing in a priming experiment, participants are usually unaware of associative / semantic influences exerted by the prime (especially at short SOAs). Still, their decision on the target can be manipulated depending on the relationship of the two words. This phenomenon of automatic predictions directly translates into the daily life of every person. For example, probably everyone has already used search engines in the World Wide Web, and was confronted with autocomplete predictions by the algorithm to improve the search quality. These predictions are closely related to co-occurrences from corpus data (the syntactically and semantically most likely next word), with further influences by global trends (e.g. entering just a “t” will show “trump” at the top) and individual search preferences (e.g. a strong interest in music will rank certain interprets and song titles much higher). Hence, research on co-occurrence statistics offers a great foundation to optimize search engines.

Other implicit priming occurs daily e.g. via advertisements or during early childhood when learning a language “automatically”. This suggests that every person’s semantic network diverges depending on outer influences like the vocabulary used by the parents. It is therefore of question whether a generalized corpus based on newspaper articles can account perfectly for all the individually different experiences. In a pilot study, Hofmann et al. (2020) collected reading data on a tablet to create individual word corpora for each of the two participants. Analyses of eye movements on controlled reading material revealed that the (comparably small) individual corpora outperformed a large norm corpus. This finding provides a first step for future studies to address the cognitive representation of a person more detailed than by relying on diary entries, for example. Moreover, it creates a picture of the personal data, which we leave when browsing the internet, and how to improve data protection.

4.10 PERFORMANCE OF FIXATION-RELATED TECHNIQUES ON READING MATERIAL

Fixation-related neuroimaging is a relatively new field in the sentence processing literature. Thus, studies, that investigated neural responses to lexical effects in natural reading, are relatively rare, but open new doors to explain previously inconclusive findings (see section 4.11). This section discusses the benefits and the issues of using several fixation-related neuroimaging techniques like fNIRS, fMRI or EEG in hindsight to the observations in STUDY C.

On paper, fMRI and EEG outperform fNIRS by their either better spatial or temporal resolution. Hence, it seems as if fNIRS stands in the middle of both, without any clear merit for the investigation of natural reading behavior. Next to the more general benefits from fNIRS over other neuroimaging techniques, like less environmental constraints or lower costs, the results of STUDY C emphasize its utilization in natural reading research on a critical point: Having a high temporal resolution to disentangle foveal from parafoveal influences, while also relying on hemodynamics.

Regarding the findings of coregistering EEG with eye movements, all conducted studies, so far, struggled to observe even standard main effects of word frequency in their EEG data (Degno et al., 2019; Himmelstoss et al., 2019; Kretzschmar et al., 2015). The absence of frequency effects could not only be observed in the N400 component (where word predictability effects dominate), but also in other time windows (Degno et al., 2019). Degno et al. (2019) were unable to provide any answer for that missing effect, whether it may be related to the experimental design or the applied methodology. When looking at predictability effects, another issue emerges for fixation-related EEG studies. Brain signals to word predictability are usually captured by the N400 component in single word studies, thus 400 ms after stimulus exposure. At an average fixation duration of ~250 ms during whole sentence reading (Rayner, 1998), lexical effects by the following word can therefore overlap with the effects from the currently fixated word. This convolution of target and pre-target fixation further challenges any investigation on PoF effects (Dimigen et al., 2011; Himmelstoss et al., 2019).

Frequency and predictability main effects could be captured successfully by fixation-related fMRI, although predictability seems to be more elusive (Schuster et al., 2016; 2020). In addition, Schuster et al. (2016) reported indications for a (non-lexical) PoF effect in the left MTG and the bilateral occipital cortex on skipping behavior. Any analyses of PoF effects by word frequency or predictability were not performed, as they were not in the focus of that research. Furthermore, analyzing corpus data (as done in Schuster et al., 2016; 2020) instead of an experimental manipulation of a target word (cf. STUDY C; Radach et al., 2013) might have raised the concern by Angele et al. (2015) that no true PoF effects but successor effects could be observed.

Judging by the limited amount of currently available research, it appears as if BOLD signals allow a better peek into the cognitive processes during natural reading than EEG data. However, the deconvolution issue also affects fixation-related fMRI (and fNIRS) studies, as hemodynamic responses take about six seconds, and interact in a nonlinear way for a quick succession of events (Binder et al., 1994; Friston et al., 1998; Huettel & McCarthy, 2000). Due to the slow rate of one functional whole-brain scan typically taking ~two seconds (cf. Schuster et al., 2016), one data point also runs the risk to refer to multiple word fixations. Moreover, Schuster et al. (2016) intentionally did not perform slice timing correction, which improved the synchronization of neuroimaging and eye movement data, but at the cost of a temporal confound on the brain data: A slice acquisition order from dorsal to ventral, for instance, suggests that activation in the dorsal and ventral regions might refer to different eye fixations.

With the goal to clearly disentangle subtle neural activations, e.g. to separate foveally from parafoveally induced lexical effects, a much higher sampling frequency (than 2 sec) seems like an unavoidable step. By reducing the spatial resolution and the covered brain regions (ROI scanning instead of whole-brain), the temporal resolution might increase sufficiently for fMRI to also address distinct lexical influences during reading. In this regard, STUDY C pioneered fixation-related fNIRS, which naturally provides more than sufficient data points to account for the nonlinearity in the hemodynamic responses.

With ten data samples per second, STUDY C demonstrated that fixation-related fNIRS can capture the lexical effect of word frequency (like fMRI), as well as highly elusive lexical PoF influences. These novel observations (particularly regarding the PoF effect) are strongly supported by the most recent theories on eye movement control (e.g. Snell & Grainger, 2019), but require confirmation by future studies, of course. Here, it may be that fixation-related fMRI – once set up accordingly (see the concerns above) – will literally give a clearer picture to this discussion.

4.11 NOVEL INSIGHT INTO NATURAL READING PROCESSES BY FIXATION-RELATED FNIRS

In a recent article on serial versus parallel processing of words, Snell and Grainger (2019, p.537) suggested that researchers should look “beyond the methodological scope of tracking eye movements”. By coregistering eye fixations to brain data, STUDY C allowed some fundamental assumptions for the natural reading research:

1) Frequency effects seem to emerge from the left visual field / left part of the word.
2) Lexical effects can influence cognitive processes as early as in the extrastriate regions of the occipital cortex, e.g. to manipulate saccade preparation.
3) Frequency and predictability may interact at an early time window.
4) By experimentally manipulating predictability and frequency of a target word, a true PoF effect on the pre-target word is observable in the eye movement and the brain data.
5) The timing of word processing during sentence reading is not tied to the OFC (cf. Hofmann et al., 2014), but might be handled by the occipital cortex and connecting regions.

The following paragraphs review these points and their implications for the current state of reading research.

1 & 2) While section 4.10 already considers the technical aspects of why the word frequency effect might be more sensitive to hemodynamic responses instead of EEG data (cf. Kretzschmar et al., 2015; Degno et al., 2019), further suggestions can be made about its origin on the basis of fixation-related fNIRS. In STUDY C, infrequent target words showed stronger neural activity in the right ventral occipital cortex (V2 region; **Fig. 10** right), thus relying on information from the left visual field due to the retinotopic organization of that region. As first fixations on German noun words were investigated, the left visual field contained a highly salient part because of the uppercase first letter (cf. Hyönä et al., 1989; Rayner & Schotter, 2014). This allowed the right ventral occipital cortex to extract lexical information very early, which is in line with the observed occurrence of frequency effects already 110 – 145 ms after fixation onset (Himmelstoss et al., 2019; Kliegl et al., 2004; Reingold et al., 2012). Predictability effects, on the other hand, emerge as late as 200 – 250 ms after the first fixation landed (Calvo & Meseguer, 2002; Himmelstoss et al., 2019; Kliegl et al., 2004; Rayner et al., 2004). It is therefore not entirely surprising that no predictability main effect was found in the occipital cortex (but see the interactive effect discussed further below). It is likely that such an effect unfolded in higher order brain regions (namely the MTG and LIFG; cf. Schuster et al., 2016), which were not captured by the optode placing, but are strong candidates for future investigations.

The V2 region was brought in functional connection with the V4 area to plan the following saccade (Mazer & Gallant, 2003; Saber et al., 2015). STUDY C suggested that a low frequency word might have induced a delay on saccade preparation, essentially to allow the higher cognitive processes more time for evaluation (Reilly & Radach, 2006). This is further indicated by considering that the significant area of the frequency main effect was very close to the fusiform gyrus, hence probably following the ventral visual route to the MTG and LIFG. Importantly, the initial unit activation in the orthographic layer of the AROM and its predecessor, the MROM (Grainger & Jacobs, 1996; Jacobs et al., 1998), is manipulated by the frequency of the corresponding words. Thus, low frequency words take longer to reach the activation threshold, similar to the present brain data, supporting the proposal by Hofmann and Jacobs (2014) that the orthographic layer represents the function of the fusiform gyrus. Moreover, it shows that the AROM is suited well to also predict neural responses to whole sentence processing.

3) An interaction of frequency and predictability in reading is highly controversial, as most studies on eye movements showed that frequency effects occur earlier and independently from predictability effects (e.g. Kliegl et al., 2004; Rayner et al., 2004; Slattery et al., 2012; Staub, 2015). Sheridan and Reingold (2012) provided evidence for influences by predictability at a similar time window like frequency, but mentioned that both variables could still exert additive effects. Hence, the EZ-Reader model addresses frequency and predictability in the first stage of lexical processing (L_1) to contribute additively to the fixation duration (Reichle et al., 2009; Schotter et al., 2014).

   Hand et al. (2010) challenged the widely accepted view of strict additivity by demonstrating that frequency and predictability can interact if the pre-target fixation was located close to the target word. Slattery et al. (2012) criticized this methodology, because a) the distance as post-hoc factor cannot be under full experimental control, and b) the number of available data points for each condition can differ a lot. In **Appendix A** of STUDY C, launch distance (Near/Far) was added as post-hoc factor to offer some comparisons to Hand et al. (2010), while also suffering under the aforementioned issues. Eye tracking data revealed a significant interaction of frequency, predictability and launch distance. Only at a near pre-target fixation, a predictability effect occurred if the target word was very frequent. This observation was also prominent for launch distances of medium and small size in the analyses of Hand et al. (2010). Kretzschmar et al. (2015) reported a similar interaction on pre-target fixations, but did not control the word preceding the target during stimulus creation. Considering the collective evidence, it does not seem completely unlikely that, despite the methodological criticisms, both properties can interact on early eye movement measures. By manipulating the parafoveal preview, Sereno et al. (2018) further reported an interaction of frequency and predictability at a valid preview, only. They suggested that a high predictability allowed a rapid top-down driven selection among the expected words, which was more efficient for frequent words that were parafoveally perceived. Thus, frequency and predictability effects were either additive or overadditive, depending on the preview and the predictability.

Looking at the latest results, it appears as if interactive effects of frequency and predictability are often concealed in eye movement data unless another factor is manipulated as well. If this holds true, this poses an issue for models that assume a strictly serial processing of lexical information, but supports PG models like the OB1-Reader, which allows overadditive effects of both variables (Snell et al., 2018). At this point, Snell and Grainger (2019) and Himmelstoss et al. (2019) come to similar conclusions: Direct measures of word recognition speed (= eye tracking data), alone, might not be sufficient to unravel all lexical influences. An alignment to neural responses, however, could bring light into the dark. Consequently, the brain data in STUDY C confirmed previous assumptions about an early interaction of word frequency and predictability. Here, infrequent words showed a predictability effect, while the preceding word was still fixated (see next point).

4) Lexical influences from the next word on the currently fixated word were also on debate, as they could point towards parallel processing of multiple words, which might contradict with the architecture of SAS models. In response to recent findings of lexical PoF effects (e.g. Radach et al., 2013), Schotter et al. (2014) included a mechanism to the EZ-Reader model, which allows a switch of attention to the next or even second next word before a saccade is performed. It is therefore possible for the model to acquire early lexical information from the parafovea during the pre-target fixation. However, this information is largely limited to bottom-up driven processes like the frequency effect, whereas predictability-based PoF effects cannot be captured reliably. Such an influence from the predictability of the following word was observed already by a few eye tracking studies (e.g. Hand et al., 2010; Hawelka et al., 2015; Kliegl et al., 2006), and replicated by STUDY C: A highly predictable target word decreased the fixation duration of the preceding word. By utilizing an experimental manipulation of a single word from the sentence, the concerns from Angele et al. (2014) about true PoF effects versus successor effects was furthermore addressed. The target words were either predictable or unpredictable, but the remaining sentence structure was identical. Moreover, the target position in the sentence was matched across the conditions, as word position contributes to first fixation duration independently from predictability and evokes distinct neural response patterns (Schuster et al., 2020). The difference in processing speed of pre-target fixations due to high versus low predictable target words could therefore only emerge from the lexical property of the target.

The brain data of Study C further revealed a PoF effect in the left dorsal occipital cortex (V3 region; **Fig. 10** left). When the target word was infrequent and unpredictable, neural activation in that region was significantly increased at the fixation of the previous word. While reviewing the points 1 & 2), it was mentioned that predictability (as late top-down driven process) probably affected higher order brain regions during the target word fixation, but not the occipital cortex. The interactive influence of predictability and frequency on the preceding word suggests a quick first peek into both lexical properties, e.g. to determine the direction of the saccade (Snell et al., 2018). This parafoveal peek cannot reliably be captured solely by eye movement measures, but seems to occur in addition and prior to the additive component of word frequency and predictability when the target is fixated. This assumption would explain why some studies found predictability-related effects at very early time windows (e.g. Hand et al., 2010; Sereno et al., 2018; Sheridan & Reingold, 2012), while the general consensus points towards a later processing of predictability (Calvo & Meseguer, 2002; Himmelstoss et al., 2019; Kliegl et al., 2004; Rayner et al., 2004). Accordingly, the EZ-Reader consists of two lexical stages (L_1, L_2) to account for early and late effects, but appears to be compromised by the serial processing approach, which neglects early top-down influences.

5) Hofmann et al. (2014) emphasized the OFC as critical region to time word processing during RSVP tasks. Here, every word of a sentence was shown in serial without any parafoveal input and no natural control to perform saccades. As a result, more difficult words could not be fully processed within a fixed duration of 250 ms stimulus presentation. Thus, to prevent bottom-up interferences by the following word on top-down predictions to the previous word, activation in the OFC increased. Switching to whole sentence presentation, as conducted in STUDY C, neural responses in the OFC no longer differed in the conditions. Interestingly, the observed interaction of frequency and predictability moved from the OFC (Hofmann et al., 2014) to the left dorsal occipital cortex (STUDY C). It might be that saccade planning by the occipital cortex had a similar purpose of distributing the cognitive processes like the timing by the OFC.

   The shift from OFC to dorsal occipital cortex activation might also help on the discussion whether lexical processing of multiple words can occur in parallel or in serial. When reading an entire sentence, the proposal of STUDY C was that the dorsal occipital cortex could time saccade preparation based on parafoveal lexical information. Such information would be available at a time when SAS models should have no / limited access to it. Importantly, the location of the effect indicates a connection towards the parietal cortex. This occipito-parietal area is considered to contain a spatiotopic map to keep track about where stimuli like the words within the perceptual span are located (Duhamel et al., 1992; Merriam et al., 2003). Spatiotopic updates occur already 150 ms after a saccade was performed, and can directly facilitate or inhibit the postsaccadic perception (Fabius et al., 2016; 2019). Hence, it is plausible to assume that parafoveal lexical information was available fast enough to influence the currently fixated word. Correspondingly, the most recent PG model, the OB1-Reader, includes spatiotopic representations to create an expectancy about the length and the number of the in parallel perceived words (Snell et al., 2018). This allows the model to store the processing order of multiple words, which addresses one of the main arguments against parallel processing that words might not be recognized in the correct order. Such a routine would not be necessary in RSVP tasks, or more generally, if words were processed serially. Any occipito-parietal finding, however, supports its inclusion when modelling sentence reading. Should future studies on natural reading provide more evidence for occipito-parietal effects, other models on eye movements consequently might want to adopt the mechanism of the OB1-Reader as well.

5 CONCLUSION

This doctoral thesis employed novel methodologies for the investigation of semantic and lexical effects during visual word recognition.

Word co-occurrences were used to separate direct associations from semantic relationships. Next, these co-occurrences were tested on the performance of a recent interactive activation model, the AROM, which includes a semantic layer to address the relationship between words. Simulation data of a primed lexical decision task demonstrated a significant prediction of response times, when direct association, semantic similarity and the SOA between prime and target are manipulated. Importantly, the performance of the AROM could be improved at long SOAs by implementing a recurrent routine to maintain semantic short-term effects by the prime word.

Neuroimaging data on the primed lexical decision task showed a strong functional connection of the LIFG to the fusiform gyrus and the hippocampal system during the resolution of semantic conflicts. The fusiform gyrus was previously suggested to integrate orthographic information, while its anterior part is already involved into semantic processing. Accordingly, the orthographic and the semantic layer of the AROM are in direct exchange of information. The linkage of the LIFG to the hippocampus further led to the addition of a conjunctive layer to the AROM. Thus, the c-AROM is now able to account for false memory effects with the principle of pattern separation as it occurs in the dentate gyrus, a subregion of the hippocampus.

The present thesis also examined multiple priming and lag priming effects on the basis of word co-occurrences. For multiple priming, regression analyses indicate that only a direct association to the preceding prime reduces the response time of the target, while a semantic relationship affects the target not until the third last prime. Looking at lag priming, a similar temporally diverging pattern of direct association and semantic similarity was observed. Direct associations were most effective at a lag of one unrelated stimulus. Semantic relationships influenced the target recognition at a lag of two. The difference between when direct associations and semantic relationships take effect, corresponds well to the spreading activation theory: Direct neighbors in the semantic network are reached faster than indirect connections.

The influence of lexical effects, namely word frequency and predictability, during natural reading was investigated via fixation-related fNIRS. The coregistration of word fixations and hemodynamic responses revealed strong evidence for the parallel processing of the currently fixated word and the following word. Activation in the left occipital cortex increased if the next word was of low frequency and low predictability. Hence, high order information from the right parafovea was used to modulate the processing speed of the fixated word. Such parafoveal-on-foveal effects are highly controversial in the eye movement literature, as they appear to be elusive in the fixation data. When utilizing neuroimaging techniques however, the present findings suggest their existence.

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