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Visual and linguistic components of short-term memory: Generalized Neural Model (GNM) for spoken and sign languages

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ABSTRACT

The question of apparent discrepancies in short-term memory capacity for sign language and speech has long presented difficulties for the models of verbal working memory. While short-term memory (STM) capacity for spoken language spans up to 7 ± 2 items, the verbal working memory capacity for sign languages appears to be lower at 5 ± 2 . The assumption that both auditory and visual communication (sign language) rely on the same memory buffers led to the claims of impairment of STM buffers in sign language users. Yet, no common model deals with both the sensory and linguistic nature of spoken and sign languages. The authors present a generalized neural model (GNM) of short-term memory use across modalities, which accounts for experimental results in both sign and spoken languages. GNM postulates that during hierarchically organized processing phases in language comprehension, spoken language users rely on neural resources for spatial representation in sequential rehearsal strategy, i.e., the phonological loop. The spatial nature of sign language precludes signers from utilizing a similar ‘overflow’ strategy, which speakers rely on to extend their STM capacity. This model offers a parsimonious neuro-architectural explanation for the conflict between spatial and linguistic processing in spoken language, as well as the differences observed in STM capacity for sign and speech.

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1. Introduction

The question of apparent discrepancies in short-term memory capacity for sign language and speech has long presented difficulties for understanding the relevance of sensory vs linguistic aspects of the input for short-term memory buffers. While short-

term memory capacity for spoken language spans up to 7 ± 2 items (Miller, 1956), the short-term memory (STM) capacity for sign languages appears to be lower at 5 ± 2 (Gozzi et al., 2011; Bavelier et al., 2001; Bavelier, Dye, & Hauser, 2006; Bavelier, Newport, Hall, Supalla, & Boutla, 2006; Bavelier, Newman, Mukherjee, Hauser, Kemeny, Braun, et al., 2008; Bavelier, Newport, Hall, Supalla, & Boutla, 2008; Emmorey & Wilson,

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2004; Marschark & Mayer, 1998; Hall & Bavelier, 2010, 2011; Pavani & Bottari, 2011; Rudner, Andin, & Rönnerberg, 2009; Geraci, Gozzi, Papagno, & Cecchetto, 2008; Wilson & Emmorey, 2006a, b; Boutla, Supalla, Newport, & Bavelier, 2004). The known discrepancy between working memory span in speakers and users of sign languages has been used to suggest that signers' IQ is inferior (Conway, Pisoni, & Kronenberger, 2009), attributed to the internal structure of signs (Bellugi & Fischer, 1972; Bernstein-Ratner & Wilbur, 1984; Geraci et al., 2008), or the differences in rehearsal strategies (Hall & Bavelier, 2010, 2011; Malaia & Wilbur, 2014). At the same time, multiple studies note that the 'hearing advantage' in STM capacity disappears in visuo-spatial tasks (Geraci et al., 2008, *inter alia*). Thus, signers' disadvantage in STM capacity seems to be restricted to linguistic tasks, in which signers and speakers rely on different modalities. Importantly, STM capacity differences connected to the use of spoken vs sign language are preserved in ASL-English bilinguals (Hall & Bavelier, 2011), i.e., the same individuals display different memory spans as a consequence of which linguistic modality they are using. Thus, it is the visuo-spatial processing modality of sign language, rather than the hearing status of the participants, that is key to understanding the phenomenon (Bross & Sauerwein, 1980; Campbell & Wright, 1990; Dye et al., 2007; Emmorey et al., 2003, 2011, 2013; Emmorey & McCullough, 2009; Finney et al., 2001, 2003; Finney & Dobkins, 2001; Hauser et al., 2007; Klima et al., 1999; Neville & Lawson, 1987; Proksch & Bavelier, 2002). We propose a neurally-grounded model of STM use in communication (spoken and signed), which provides a parsimonious account of behavioral and neural (fMRI) data on STM buffers use in communication.

While multiple behavioral and neural models of working memory have been proposed and refined for *spoken languages* (e.g., Baddeley 1984, 2012; Öztekin, Davachi, & McElree, 2010), few have addressed the *difference in use of both general and specific memory resources necessary for sign language processing*. We address the apparent discrepancy in STM capacity in signers and speakers by modeling the differences in demands on specific neural resources imposed by modality differences between signed (visuo-spatial) and spoken (auditory) language.

In the following, we review investigations of sub-components of working memory in signers, and propose a model for the neural architecture for visuo-spatial working memory (visual WM). We discuss evidence supporting reliance of sequential encoding strategy in speakers – aka “the phonological loop” – on spatial processing resources, and argue that it is the conflict with presence of spatial parameters in signs that leads to seemingly lower WM span for signers. In fact, we should consider the reverse logic, as evidence suggests that the use of a sequential encoding strategy for non-spatial (auditory) stimuli leads to *inflated* WM spans for non-signers (Bavelier, Newport, et al., 2008), and then, only under certain conditions. With this in mind, we use the dual executive processing model (Nee et al., 2013) to offer an explanation for this puzzle of verbal working memory capacity in signers and speakers, highlighting the aspects of the psychophysiological profile in signers that are important for further informing development of visual working memory models. Our model of STM use in communication dissociates between sensory and linguistic aspects in communication, clarifying that the same neural resources are recruited for

sequential rehearsal (phonological loop) and also for spatial representation. We thus provide a parsimonious explanation both for spoken and sign language data. In addition, the model resolves the conflict between spatial and linguistic processing in monolingual users of spoken language alone.

2. Sensory and linguistic parameters of sign language input: implications for STM models

Before considering applications of different STM models to the issue of possible reduced WM span in sign language users, it is important to consider the nature of the sign language signal, which determines the resources required for visuo-spatial and linguistic processing. Here, we briefly review the structure of sign languages and how they compare and contrast with spoken languages. We also consider how the inference that signers have reduced memory span has been reached, and review various explanations for it that have been offered to date.

2.1. Sign languages as linguistic systems

Sign languages are linguistic systems which utilize handshapes, hand position, body, facial articulators (e.g., brow positions, mouth shapes), and hand motion to communicate information at multiple levels of the linguistic system: phonology,¹ morphology, syntax, semantics, and pragmatics. Standard analysis of lexical signs posits four basic parameters of the manual signal: handshape (HS), orientation of the palm and fingers (O), place of articulation (POA), and movement (MOV). For each of these, minimal pairs (or triplets) can be constructed (Fig. 1).

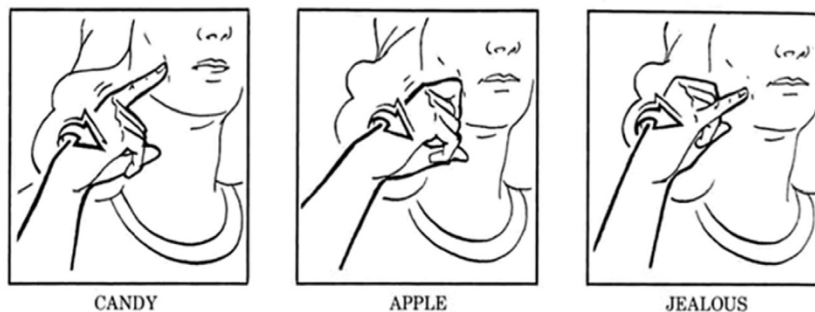
The visual signal that is used for sign language communication varies meaningfully along two dimensions, spatial and temporal, in ways that are not observed for spoken languages. Given the visual nature of the linguistic signal, signers use lexical memory to bind separated visual features of input into meaningful components in all meaningful dimensions. This use of spatial information by the signed input modality represents an important difference concerning the requirements that sign languages impose on short-term memory, as compared to spoken languages.² While auditory input composed of frequencies at varying amplitudes varies with time only, the signed visual signal composed of moving hands changing locations and handshapes varies both in time (as to *what* is perceived) and in space (*where* in space the hand is located at each point in time).³

¹ Phonology in sign language refers to minimal distinctive visual features, such as handshape, hand location, orientation, or type of movement (Brentari, 1998).

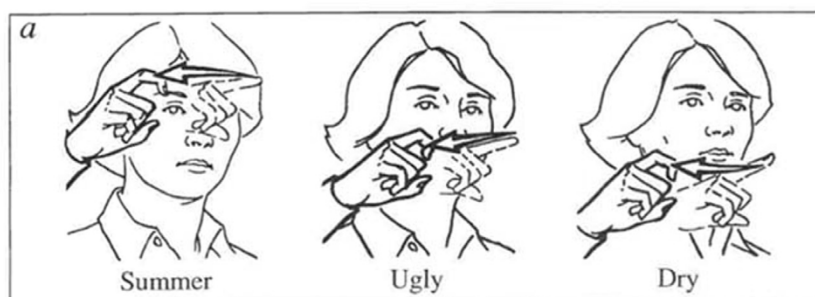
² Identification of sound source for spoken languages, which arguably involves spatial processing, is not relevant to linguistic communication in the same way as identification of morphemic content from spatial sign location in ASL.

³ The same handshape ‘5’ (an open palm with outstretched fingers), when used in different positions on the face – chin vs forehead – in ASL means, respectively, “mother” and “father”. Addition to these static signs of an arc motion away from the body indicates addition of a generation – “grandmother” and “grandfather”. Also, we are not addressing non-manual channels (face/head/body) for simplicity.

Minimal pairs for Handshape: CANDY, APPLE, JEALOUS



Minimal pairs for Point of Articulation: SUMMER, UGLY, DRY



Minimal pairs for Movement: TAPE, CHAIR, TRAIN

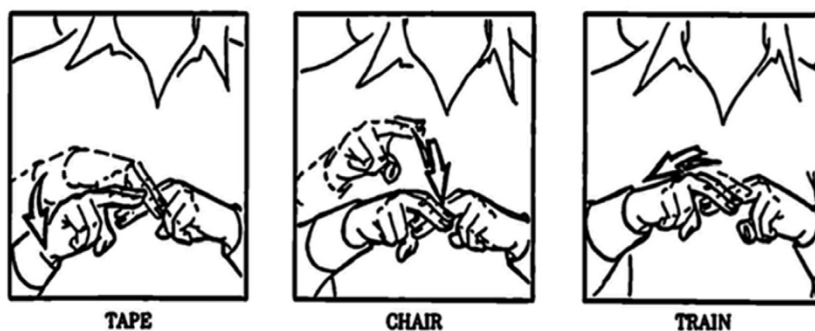


Fig. 1 – Articulatory components of lexical signs: Handshape, Point of Articulation, Movement. Used by permission Ursula Bellugi, The Salk Institute for Biological Studies.

Memory strategies for signing appear to be quite similar to those for speech. It is known that signed similarity on phonological parameters causes interference parallel to what is observed for speech, and that suppression of possible manual articulation affects retrieval (Wilson & Emmorey, 1997; Wilson & Emmorey, 2000). In parallel to observations for speech, the increase in the length of signs, and presence of irrelevant signing have a detrimental effect on memory performance (Wilson & Emmorey, 1998, 2003). Thus, signers display parallel reliance on phonological encoding and some sub-articulatory mechanism for sign rehearsal. Prior explanations offered for observed reduction in STM in sign language users have included differences in duration between spoken/written words and signs. This has been refuted by several experimental studies (Geraci et al., 2008; Hall & Bavelier, 2010).

Geraci et al. (2008) manipulated spoken word length for a hearing group and shorter sign length for a deaf group, as well as

manipulating production speed for both groups. On measurement, there was no significant difference in duration between speech and sign (in conversation for both speech and sign, the average syllable duration is about quarter of a second; Wilbur & Nolen, 1986; Wilbur & Malaia, 2008). From this, Geraci et al. suggested that either the capacity measured by standard STM measures is not involved in language processing (Waters & Caplan, 2005) or that STM is an important component of language processing, but that sign languages have some mechanism (an ‘internal organization’) that enables them to reduce the language processing load. They prefer the second option, suggesting that it is supported by sign language use of space for grammatical purposes, which eliminates separate signs for various functions (such as pronouns, prepositions, determiners), reducing the number of signs in the input and the load on the memory buffer. In addition, the use of grammatical facial expression for negation, conditional clauses (‘if’), among

others, likewise reduces the number of independent signs necessary in each sentence.

Hall and Bavelier (2011) indicated that item order is critically involved in STM performance in signers: if serial order is not relevant, STM span differences between signers and speakers are less noticeable. However, when serial order is important to the task (i.e., rehearsal of working memory content is necessary), the difference in STM performance between signers and speakers becomes significant. In an overview, Hall and Bavelier (2010) suggested that the source of the difference in serial recall is not a generalized temporal ordering problem in signers, but instead, a tendency for speakers to rely on rote rehearsal of speech-based representations. They suggested that this may be related to the distribution of load between the two neural pathways involved in visual memory, dorsal (for location) and ventral (for objects). Experimental comparison of serial vs free recall in signers of Catalan Sign Language, and speakers of Spanish (Alba, 2016), also indicated that use of item order in STM maintenance provides advantage to non-signers, as compared to signers.

We propose a generalized neural model of memory use across modalities (GNM) to account for this discrepancy of verbal working memory that stems from differing modality requirements of speech and signing. Specifically, we identify neurocognitive differences in STM buffering for speech and sign: a ‘sequential rehearsal’ strategy available for auditory processing, and we offer an explanation as to why it is not available to signers for use in rehearsal. We focus on empirical evidence for competition between executive maintenance and manipulation of spatial representation that is inherent in sign languages, but not in spoken ones. In the following sections, we review the current debate over the modality tradeoffs in working memory capacity, hemispheric lateralization of processing components, and executive control for linguistic processing. We demonstrate that application of a dual-stream executive processing hypothesis yields a non-conflicting account of visual working memory capacity in signers and speakers.

2.2. Structure of visual-verbal working memory: behavioral evidence

The most widely-used model of working memory (see Baddeley & Hitch, 1974; Baddeley, 2012, for a recent revision), makes a distinction between two different short-term memory buffers – auditory-based working memory and the visuo-spatial sketchpad—based on the input modality difference and the connection of input to language. Behavioral research on the structure of verbal working memory indicates that most of the temporal, motor, and feature-based effects in verbal working memory for spoken languages have also been documented for sign language. These include the phonological similarity effect (Wilson & Emmorey, 1997), articulatory suppression effect (Wilson & Emmorey, 1997; Wilson, 2001), primacy and recency effects (Bellugi, Klima, and Siple, 1975), and the interference effect from irrelevant speech (or motion for signers) (Wilson & Emmorey, 1998, 2003).

In the perceptual domain, sign language users appear to have the same neural temporal resolution for input signals (Bross, 1979; Poizner & Tallal, 1987), combined with better motion

processing in the peripheral visual field (Bosworth & Dobkins, 1999, 2002; Bosworth, Petrich, & Dobkins, 2013; Swisher, 1989; 1990). These advantages in perception in signers appear to be due to enhanced executive processes of attention-allocation, attention-switching, and response inhibition in the visual domain (Brozinsky & Bavelier, 2004; Bross, 1979; see also Pavani & Bottari, 2011, for review). With regard to the executive component of working memory (WM), signers significantly outperform speakers in attention-switching (Colmenero, Catena, Fuentes, & Ramos, 2004), and visual manipulation abilities (Springford, 2006). In the experiment that used the Corsi Block Test for visuo-spatial short-term working memory, Geraci et al. (2008) showed that age-, gender-, and education-matched deaf participants significantly outperformed the hearing participants.

Enhanced attention-switching in signers appears to be related to perceptual filtering enhancements needed to deal with source simultaneity in sign languages, such as the layering of multiple non-manuals over sequences of signs. For example, Liddell (1978) observed that a non-manual marker for yes/no questions (‘brow raise’) could scope over an entire question with an adverbial mouth expression (‘mm’, meaning “with ease”) contained inside and only covering the signs actually inside the verb phrase. Wilbur (2000) argued for pervasive layering of upper and lower face over different syntactic domains, and it has been recently observed that this is even more systematic with respect to Cinque’s (1999) hierarchy of adverbials in German Sign Language (and possibly universally) (Bross & Hole, 2017). This layering requires that each such marker be perceptually distinct so as not to be confused or lost while co-occurring with other grammatical non-manuals and also affective facial expressions. Thus the simultaneity of their expression requires distinctive coding (which articulators, when the marker starts and stops), which must be noted by the viewer and presumably encoded into memory storage along with the incoming sequential signs.

Wilson and Emmorey (1997) have also shown that, although both articulatory suppression (manual motor coding for sign languages) and phonological similarity of stimuli signs interfere with recall in sign languages, their effects do not interact. This suggests that for sign languages, motor encoding and feature binding rely on separate executive components. While Wilson and Emmorey (1997) present evidence of sign rehearsal in STM task, they note that the strategy observed for sign rehearsal does not appear to have a spatial directional component (“information could be read off with equal ease in either direction”, p. 318). Miozzo et al.’s (2016) study of positional schemes used for the encoding of item order both in speakers and in signers also specified “difficulties in binding an item in visuo-spatial STM to its specific position in the sequence” for signs. At the same time, sequence-based directionality for speech rehearsal and recall, for stimuli presented either auditorily or visually, has strong experimental support (Fischer-Baum & McCloskey, 2015; Cortis et al., 2015, inter alia). This suggests that both architecturally and functionally, the rehearsal system for spoken language (phonological loop) and sign language bear little resemblance to each other. The first suggestion for a distinctly different STM maintenance mechanism for sign language, as opposed to speech, is found in the review by Cecchetto and Papagno (2011). The present analysis extends this proposal,

reviewing new behavioral and neuroanatomical evidence for different distribution of processing resources in STM maintenance for speech and sign, and presentation of potential neural paths underlying such distinct mechanisms.

In the domain of non-linguistic visual working memory, speakers' working memory capacity drops significantly when rehearsal possibility via phonological loop is controlled for. Saito, Logic, Morita, and Law (2008) demonstrated this effect on recall of Japanese Kanji characters in the visual domain. The participants in the study were shown a series of six characters and asked to write them down. They were also asked to do the same task while saying "1, 2, 3" aloud in Japanese (articulatory suppression task). The recall under the articulatory suppression condition results in a 10–20% drop in accuracy. Thus, the retention of serial order for visual and phonological information in kanji appears to be based on separate, domain-specific subsystems in speakers, with the purely visual recall (under articulatory suppression) reduced compared to visual recall with phonological encoding assistance (no articulatory suppression).

Gozzi et al. (2011) also showed that when challenged with above-capacity task (WM span +1) on serial recall tests, signers and speakers make both item errors and order errors at the same rate. Supporting this line of reasoning, Boutla et al. (2004) has shown that the increased number (up to 7 items) retained in non-signers' phonological loop is *only present in serial recall*, and thus would appear to be the result of a unidirectional, serial encoding strategy. Notably, when the option of a phonological loop-based rehearsal strategy is not available to speakers in experimental settings (as in the Kanji articulatory suppression task), performance on working memory tasks with serial recall becomes on par with that of signers, that is, speakers lose the advantage they have compared to signers. Liu, Squires, and Liu (2016) arrived at similar conclusions based on testing of encoding strategies in (hearing) bimodal bilinguals of Taiwanese Sign Language/Chinese, and ASL/English. In recall task for ordered lists, oral suppression significantly reduced STM spans, while manual suppression had no effect. Thus, bimodal bilingual participants of unrelated sign and spoken languages were relying on speech-based, rather than sign-based rehearsal to retain lists of signed items in short-term memory.

Collectively, this evidence supports the claim that there exists a directional phonological rehearsal resource that is available to speakers, and gives them the advantage in memory span. What factor, then, contributes to an apparently higher WM span in speakers in serial recall tasks and why cannot signers take advantage of this factor?

An investigation of serial-order working memory for verbal items in spoken language (van Dijck, Abrahamse, Majerus, & Fias, 2013) demonstrated that the selection of relevant information from a serial-order representation in WM is driven by an attentional search across an *internal representation of space*. In several experiment, participants were presented with a self-paced presentation of a sequence of four numbers, followed by a spatial search task for a dot inside the left or right visual field. The search was conditioned by a go/no-go task, in which a "go" response could be triggered by one of four numerals. Finally, participants responded to probes regarding sequential order of numbers presented. Response times indicated that retrieval of later items of a number sequence stored in working

memory produced covert attentional shifts toward the right: the earlier the "go" item appeared in the original presentation sequence, the faster was the dot-detection response for left-side relative to right-side dots.⁴ The numerals presented earlier in the pre-run sequence were conceptualized by participants as spatially located on the left, triggering leftward shift in spatial attention, which then influenced the search task. Since the 'internal rehearsal' of the trigger numerals utilized the phonological loop, the attentional shift provided corroborative evidence that the phonological loop in hearing participants activated spatial processing networks, leading to observed behavioral preference in space. However, such distribution of cognitive load with recruitment of spatial processing resources conflicts with the structure of sign languages, where space is routinely and consistently used for linguistic purposes (cf. Krebs, Malaia, Wilbur, & Roehm, 2018).

To understand how sign language input is routed through visuo-spatial (dorsal and ventral) processing pathways, it is necessary to consider the structure of signs. Recognition and encoding of the intended Handshape for storage and recall should be handled along the object pathway, as its features are in fact those of an object: it has shape, size, and other properties such as whether there is contact among fingers and if so, which, and whether fingers are adjacent or spread (to name but a few options). Models of Orientation in signs differ as to whether it should be considered basic or derivative from other features, but for our purposes, we may consider Orientation to also be an object property. Up to this point, we could say that the coding of Handshape and Orientation as object properties is parallel to the coding of print letters or digits. The difference with signs comes from the need to encode Place of Articulation (POA) and movement (MOV) of signs. It should come as no surprise that the location pathway is recruited to encode the location (POA) and change of location (MOV) of signs. What this means is that the initial encoding of signs, because they have POA and MOV, ties up the location pathway (spatial processing resources) even at the lexical level, so that it is not available for use as a spatial supplement to phonological rehearsal of serially-ordered material. That is, these resources are recruited initially to encode parts of what must be remembered, so they are not available to help with the remembering process (rehearsal) itself. Furthermore, beyond the lexical level, sign languages require spatial processing for direction and velocity of articulator motion in signing. Thus, the spatial processing resources are already taken up by lexical, phonological, and syntactic processing in sign language; the resource is not freely available for distribution of cognitive load on working memory as it is for speakers.⁵

⁴ Follow-up experiments in van Dijck et al. (2013) controlled both for the number magnitude, to prevent influence of the SNARC effect (Dehaene et al., 1993), and the response method, to prevent handedness bias (Newman, Malaia, & Seo, 2014).

⁵ We expect our explanation to be relevant to any studies using fingerspelling and, by extension, signed numbers. The traditional view that fingerspelling is composed of a series of handshapes is insufficient to account for its production and perception; the other parameters (orientation, place of articulation, movement) are needed as well. Evidence shows that fingerspelling is performed in syllabic chunks, and is subject to syllable structure and morpheme structure constraints in ASL (Akamatsu, 1985; Brentari, 1998).

What might this interaction between spatial attention and serial rehearsal and recall mean in terms of the neural bases in working memory structure in speakers and signers? The first possibility is that serial order representation (phonological loop) uses neural resources that can also be recruited for spatial representation. When speakers rehearse spoken language, nothing in the signal being rehearsed makes use of spatial resources. Thus, speakers can recruit spatial resources to assist with sequential rehearsal (phonological loop).

The signers, however, are not able to use spatial resources to assist with rehearsal: spatial resources are already being used to process signed input (identifying and remembering hand locations). Thus, signers do not get a strategy-based boost from serial rehearsal the way that speakers do. This line of reasoning is supported by the fact that when the rehearsal option is blocked for speakers, their WM span drops accordingly to the level observed for signers (cf. Geraci et al., 2008; Saito et al., 2008).

There is convergent neuroimaging evidence for use of spatial neural resources in phonological-loop-based memory maintenance strategy. Yue, Martin, Hamilton, and Rose (2018) have shown that speakers presented with auditory lexical items, and asked to perform a word recall task, activated left supramarginal gyrus (SMG) during maintenance delay. This specific region is peculiar in that while it is identified in neuro-linguistic literature as the locus of phonological buffer storage (cf. Papagno et al., 2017; Paulesu, Frith, & Frackowiak, 1993), the research on spatial processing identifies its direct involvement in spatial processing in non-signers (cf. Andres, Pelgrims, Olivier, & Vannuscorps, 2017; Arend, Ashkenazi, Yuen, Ofir, & Henik, 2017; McDowell, Holmes, Sunderland, & Schürmann, 2018). These findings support the account of spatial processing resources used in the phonological loop/buffer STM strategy by non-signers. In signers, SMG is engaged during linguistic processing because the language is spatial in nature. SMG is therefore not available for use in the phonological loop/buffer STM strategy (Corina & Blau, 2015; Emmorey, McCullough, & Weisberg, 2015; Newman, Supalla, Fernandez, Newport, & Bavelier, 2015).

Another process that might provide additional cognitive load in sign recall (as opposed to spoken word recall) is that the executive maintenance of verbal working memory (phonological loop) interferes with executive manipulation of visual features for creation of spatial representation. The result is competition between temporal rehearsal and serial order representation, or, more generally, spatial processing. Thus, the increased WM capacity in serial recall for users of spoken languages appears to be the result of a directional encoding strategy. This strategy does not function in the presence of visual spatial input⁶: the need for *spatial processing*

⁶ Sign languages do have phonology; however, it is spatially-based (e.g., the location of the sign is one of relevant parameters for word meaning, and can be the basis for minimal pair formation). Thus, the term “phonological loop” is misleading in application to sign languages – the availability of directional encoding strategy (aka the “phonological loop”, as known from spoken language data) would have to be conditional upon absence of relevant spatial information (which is never the case in sign languages).

appears to prevent the possibility of *serial rehearsal*, regardless of the modality of the input (as summarized in Fig. 2).

We now consider possible neural bases of this phenomenon in signers and speakers, based on dual-stream models of visual processing and executive control.

3. Generalized Neural Model (GNM): a neurocognitive model of working memory for sign language and speech

The original Baddeley & Hitch (1974) model of working memory, which has been applied to both spoken and sign languages, consisted of three components: the central executive, the phonological loop, and the visuo-spatial sketchpad. Recent advances in neuroimaging research suggest the need for increased granularity in conceptual understanding of both the memory storage, as well as the executive component responsible for memory access.

Memory storage, instead of being subdivided into short- and long-term, are currently more accurately described by neural resource-based models (Buchsbaum, Olsen, Koch, & Berman, 2005; Ma, Husain, & Bays, 2014; Oberauer, 2002). For example, in Oberauer’s 3-state model of the memory storage, the perceptual trace of the input (either auditory or visual) can reside in one of three different states, based on behavioral distinctions in the timing of access to items in memory. These states are differentially characterized by the level of neural activation, as well as accessibility of the trace to the components of the executive system. The single most active trace is in the focus of attention state (FA), immediately available for cognitive processing. Several (3 ± 1) additional items are in the direct access region (DAR) state, due to their recency; focus of attention can switch among DAR items, making one of them available for processing. Finally, a portion of long-term (semantic) memory is activated and maintained in conjunction with DAR (a state termed aLTM) (the influence of the items from the aLTM state on cognition can be observed, for example, in priming).

The executive component of working memory has been shown to follow the dual-selection model using the ventral/dorsal dichotomy in the lateral prefrontal cortex (LPFC; Nee et al., 2013; Nee and Jonides, 2013; Öztekin, McElree, Staresina, & Davachi, 2009, 2010; Barredo, Öztekin, & Badre, 2013). This model also suggested a functional distinction between the two control streams from prefrontal cortex: the dorsal stream, connecting dLPFC and parietal cortex, which appears to control the focus of attention in DAR (i.e., WM updates and intrusion resistance), and the ventral stream, connecting VLPFC and portions of temporal cortex, responsible for manipulation of working memory contents.

The neural networks used for signed and spoken language processing appear largely similar in structure, although signers rely on right-hemisphere activity to a greater extent than speakers (Newman, Bavelier, Corina, Jezzard, & Neville, 2001; Neville et al., 1998; Emmorey et al., 2002, inter alia). However, functionally, signers and speakers utilize portions of the language network differently in different stages of processing, including encoding, rehearsal, and recall (Bavelier, Newport, et al., 2008). Specifically, Deaf signers appear to have more

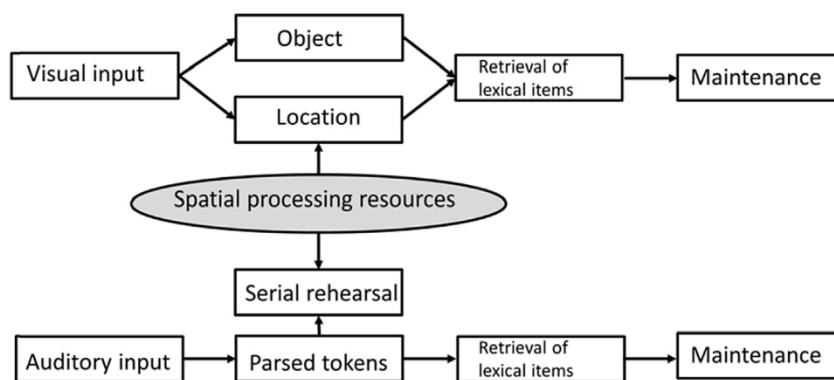


Fig. 2 – Generalized Neural Model (GNM) of memory use for auditory vs visual linguistic input: the difference lies in the use of spatial processing resources, which are required for location processing in sign language, but can be recruited to support serial rehearsal (“phonological loop”) in spoken language.

executive involvement in encoding, i.e., more use of the executive frontal network during recall. Hearing participants, on the other hand, use IPC (inferior parietal cortex) during recall more than the Deaf (likely for chunking and manipulation of information). These activation patterns are consistent with the hypothesis that encoding of spatial “where” information utilizes the regions of IPC that are used by speakers for strategic maintenance (phonological loop in rehearsal). Signers, on the other hand, use the same regions during encoding and recall (containing activation traces for “where” information) – but cannot use these regions for rehearsal. Behaviorally, this unavailability of IPC resources for rehearsal manifests as lower WM span for signs (which have the spatial component), as opposed to spoken words (which do not).

Fig. 3 summarizes what is currently known about the processing of visual input and the executive control of semantic memory. The “where” and “what” in the visual input

are processed using the dorsal and ventral pathways from the occipital lobes. This information is integrated into abstract representations (memory ‘tokens’) in the inferior parietal cortex, which can be regulated by two streams of executive connections: the dorsal, from DLPFC, regulating focus of attention and intrusion resistance, and ventral, responsible for reactivation of memory traces, and manipulation of items in the short-term memory.

It has long been hypothesized that spatial systems may be recruited for certain aspects of sign language processing (e.g., Campbell, MacSweeney, & Waters, 2008; Courtin et al., 2010; Gentner, Özyürek, Gürcanli, & Goldin-Meadow, 2013). Rönnberg et al. (2004) noted that the neural substrate for SL processing encompasses bilateral temporal, parietal, and premotor arrays—markedly similar to the neural activation observed under generation of visuo-spatial array (cf. Zago & Tzourio-Mazoyer, 2002). The dual executive processing

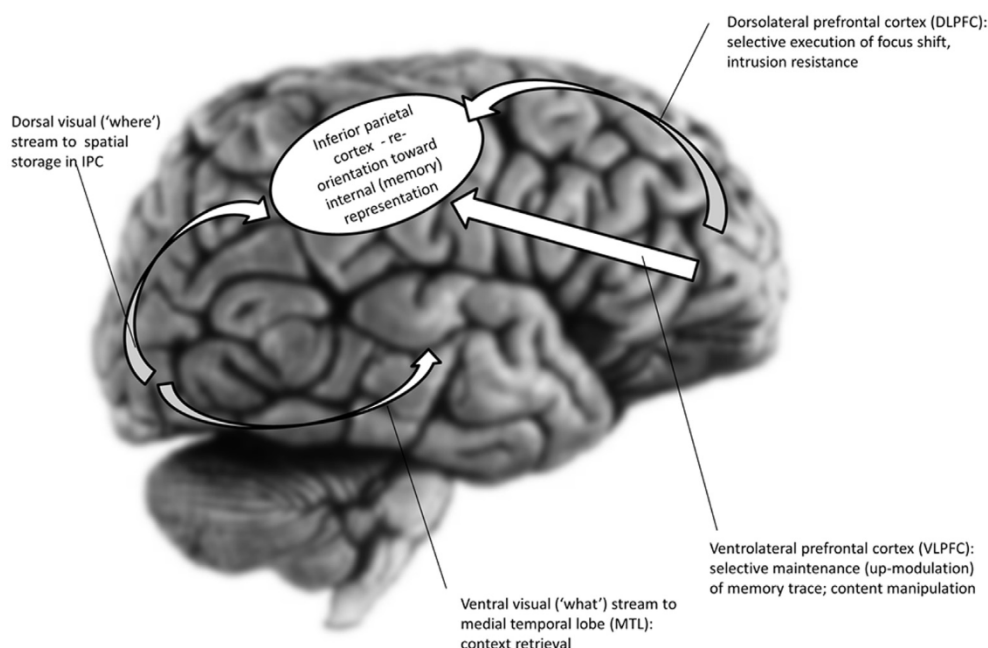


Fig. 3 – Dual-stream visual processing (dorsal “where” and ventral “what” streams) interacts with dual-stream executive processing (DLPFC “change” and VLPFC “maintain”) in the task-dependent processing of sign language.

model (Nee et al., 2013; Nee and Jonides, 2013) accounts for this data by suggesting that generation of visual WM content and maintenance of a visual-semantic percept relies either on the same executive component, or on the dorsal-parietal pathway shared by distinct components.

Alternative theories put forth to explain the differences between working memory function in sign and spoken languages typically suggest that sign language effects on memory stem at least partially from perceptual differences in the deaf vs hearing populations due to recruitment of temporal cortices in the deaf for spatial-linguistic processing (Cattani & Clibbens 2005; Cattani & Clibbens & Perfect, 2007). GNM provides a more parsimonious account for use of spatial resources in buffering for speech and sign, as well as for the conflict between spatial and linguistic processing in spoken language alone, by pointing out that the same neural resources are recruited for sequential rehearsal (phonological loop) and spatial processing.

The contribution of sign language research to the modeling of visual working memory consists both in highlighting the importance of the visual features of the communicative signal, and in clarifying the role of executive control in access to semantic memory. Remarkably, fMRI evidence indicates that even non-signers respond strongly to signed input, engaging both motion and language processing regions in response to videos of ASL signs (Malaia, Ranaweera, Wilbur, & Talavage, 2012; Malaia & Wilbur 2012, 2014), possibly due to attempts to process high information content⁷ encoded in the variability of motion in sign language (Malaia, Borneman, & Wilbur, 2016, 2017; Borneman, Malaia, & Wilbur, 2018). Further research into encoding strategies for various types of visual signal in signers and non-signers can help understand the similarities and differences in the processing of information content across modalities in human communication.

4. Conclusion

In GNM, we have offered a unified explanation for behavioral and neural data on interaction between linguistic and spatial WM from studies of hearing speakers and Deaf signing adults, by focusing on the neural basis of the relationship between the executive processing and three-state attention models. Rather than assuming existence of a single, modality-independent yet language-specific memory buffer (verbal short-term memory), we show that the input domain (visual vs auditory) affects the choice of potential strategies for enhancing STM-based performance. Specifically, we offered evidence that rehearsal component of STM in sign languages cannot use the same neural resources as rehearsal component of STM for spoken languages. Our analysis shows that signers' short-term memory is not impaired, as has been claimed in the literature (cf. Conway & Christiansen, 2005). Instead, short-term memory for spoken language can be boosted when users are able to tap into neural resources otherwise reserved for spatial processing (unless those resources are engaged by spatial processing tasks). These

strategies are unavailable to signers, as sign language processing engages the same neural resources.

In addition to resolving the puzzle of memory span differences between sign and spoken language as domain-specific, rather than language-specific, GNM demonstrates the connections among the neurobiological underpinnings of memory, attention, and executive control through the sharing of the neural resources.

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⁷ Potential information measured as Shannon information in the signal.

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