TMS Interference with Primacy and Recency Mechanisms Reveals Bimodal Episodic Encoding in the Human Brain

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Abstract

■ A classic finding of the psychology of memory is the "serial position effect." Immediate free recall of a word list is more efficient for items presented early (primacy effect) or late (recency effect), with respect to those in the middle. In an event-related, randomized block design, we interfered with the encoding of unrelated words lists with brief trains of repetitive TMS (rTMS), applied coincidently with the acoustic presentation of each word to the left dorsolateral pFC, the left intraparietal lobe, and a control site (vertex). Interference of rTMS with encoding produced a clear-cut double dissociation on accuracy during immediate free recall. The primacy effect was selectively worsened by rTMS of the dorsolateral pFC, whereas recency was selectively worsened by rTMS of the intraparietal lobe. These results are in agreement with the double dissociation between short-term and long-term memory observed in neuropsychological patients and provide direct evidence of distinct cortical mechanisms of encoding in the human brain. ■

INTRODUCTION

The serial position curve is a classical finding of the experimental psychology of memory (Capitani, Della Sala, Logie, & Spinnler, 1992; Ebbinghaus, 1885/1964; Kirkpatrick, 1894). Items presented at the beginning and at the end of a sequence are typically better recalled than those in the middle (e.g., Bennet & Murdock, 1962). Such an advantage for early and late items is known, respectively, as *primacy* and *recency* effect. An influential interpretation of serial position effects (Atkinson & Shiffrin, 1968) attributes the U-shape of the free recall curve to the functioning of two separate memory stores: a limited-capacity short-term store (STS) and a long-term store (LTS). At the beginning of recall, the final few items are residing in the short-term buffer and can be accessed immediately. The remaining items are then retrieved from the LTS (Atkinson & Shiffrin, 1968; Glanzer, 1968; Waugh & Norman, 1965). The dual-store approach was supported by experimental manipulations that differentially affect recency and primacy effects (for reviews, see Wickelgren, 1973; Glanzer, 1968). For example, recency is abolished when participants are engaged for a few seconds in a distractor task after a list presentation (e.g., Glanzer, 1968) or when they are asked to recall words from the beginning of the list (Dalezman, 1976), whereas primacy can be affected by an increase of the number of items in a given list or of the presentation rate (Raymond, 1969; Bennet & Murdock, 1962).

In the framework of the classical "modal" model of memory (Atkinson & Shiffrin, 1968), the process of passing information through the STS to the LTS is considered as an obligatory stage for external incoming items. This idea has not gone unchallenged. Single-storage theories have been postulated on the basis of behavioral studies (Howard & Kahana, 1999; Neath, 1993). According to these interpretations, position-related differences in recall could be explained within a single memory store concept on the basis of ease of discriminability in memory between early and late items (Neath, 1993; Glenberg et al., 1980) or of contextual overlap between study and test items (e.g., Howard & Kahana, 1999).

Neuropsychological findings have played a crucial role in supporting the dual storage theory (Baddeley, 2000). Primacy but not recency is affected in the amnesic syndrome, which is characterized by an impairment of long-term memory (Baddeley & Warrington, 1973). Crucially, the reverse dissociation has also been reported. Patients with a selective disorder of the STS showed an abolished recency effect, whereas primacy was preserved (Basso, Spinnler, Vallar, & Zanobio, 1982; Shallice & Warrington, 1970). This evidence was in contrast with the "modal" model.

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In the absence of an adequate STS, information should be rapidly lost, preventing any possibility to learn new information. In fact, these patients had normal long-term learning and no evidence of cognitive impairment. These observations were instrumental for the development of the multicomponent working memory (WM) model (for a recent summary, see Baddeley, 2010). Within this framework, incoming information gets an obligatory access to limited capacity, temporary stores characterized by shallow encoding of the stimuli. Parallel, deep encoding is responsible for the long-term retention of meaningful information, which is only modestly affected by defective temporary storage.

It should be noted that dual encoding mechanisms are also compatible with a single memory store. Blumenfeld and Ranganath (2006) underlined that tasks typically used to assess STM and long-term memory (LTM) are different. The span tasks used to assess phonological STM require the immediate recall of sequences of digits. A typical LTM task requires the learning of lists of meaningful words across multiple learning trials. A crucial test is thus the ability of patients with phonological STM deficits to learn information that is difficult to encode semantically or visually. The available evidence indicates that patients with phonological STM deficits are severely impaired in learning nonwords (Baddeley & Wilson, 1988), indicating a dissociation between encoding mechanisms rather than between memory stores.

Despite of a bulk of neuroimaging studies that supported a dual storage model (Fletcher & Henson, 2001), a unitary view of memory, conceived as a continuum with structures showing increased recruitment as memory demands increase, by variables such as retention time, is also supported by a study of Nee and Jonides (2008). Activation of the medial-temporal lobe structures and pFC were observed also in the case of STM items, with the only exception of the most recently presented item, suggesting that the same retrieval mechanisms used for long-term retrieval are also engaged in the case of STM items that are outside the attentional focus.

It remains that neuroimaging data are correlational and that causal evidences demonstrating one of the two models are still lacking in healthy humans. Therefore, in this study, we applied repetitive TMS (rTMS) to test the specific encoding mechanism predicted by the multicomponent WM model. We reasoned that rTMS interference with the left dorsolateral pFC (DLPFC), which exerts a top–down hierarchical control on the hippocampal formation in encoding operations (Simons & Spiers, 2003) and is particularly susceptible to rTMS-induced disruption of episodic memorization processes (Rossi, Innocenti, et al., 2011; Feurra, Fuggetta, Rossi, & Walsh, 2010; Innocenti et al., 2010; Rossi et al., 2001, 2004, 2006; Floel et al., 2004; Rami et al., 2003; Sandrini, Cappa, Rossi, Rossini, & Miniussi, 2003), might impair subsequent recall for early memorized items, possibly leaving an unaltered recency recall. We also expected that disrupting the left intraparietal lobe (IPL) activity at encoding, which is mainly involved in short-term memorization (Greve, Doidge, Evans, & Wilding, 2010; Nee & Jonides, 2008; Dudukovic & Wagner, 2007; Talmi, Grady, Goshen-Gottstein, & Moscovitch, 2005), might impair recency recall, possibly leaving an unaltered memory trace of early memorized items.

In an event-related design, brief trains of rTMS were applied to the left DLPFC, to the left IPL, and to a control brain region during encoding of 20 lists of 20 words presented in auditory form. Immediately after the presentation of each list, participants were requested to perform a classical free recall test. This design allowed to assess the interference effect of rTMS on the memorization ability according to the serial position curve and to directly demonstrate the causal role of the stimulated cerebral areas in these processes.

METHODS

Participants

Thirteen healthy volunteers (six women; mean age = 27.8 years, range = 19–37 years), screened for TMS suitability (Rossi, Hallett, Rossini, & Pascual Leone, 2011), with no history of implanted metal devices, neurological or psychiatric diseases, or drug abuse, were included in the study. All participants were right-handed according to the Edinburgh handedness inventory (mean dexterity index = 90%, range = 80–100%). The study was performed according to the Declaration of Helsinki, and the local ethics committee approved the use of rTMS. All participants gave their written informed consent and were asked to report any adverse effects experienced during or after rTMS. The experiment could have been stopped at any time, on participants' demand.

Experimental Protocol

Participants were seated in a comfortable chair, wearing headphones connected to a personal computer. Twenty lists of 20 unrelated Italian high-frequency words, ranging from 4–12 letters in length, were prepared and stored through E-Prime presentation software (Psychology Software Tools, Inc., Sharpsburg, PA). During the experiment, words were presented acoustically (with an interword interval of 2 sec) via headphones. Immediately after the end of the presentation of each list, participants were asked to recall as many words as they could. The test task was an immediate free recall with no reasonable time limit for the participants.

For each participant, the 20 lists of words were randomly assigned to one of four experimental conditions (five lists/100 words/condition), and they were run in a random and counterbalanced fashion: baseline (no rTMS), rTMS to the left DLPFC, rTMS to the left IPL, and rTMS to the vertex (control site).

Depending on the participants' free recall speed, the whole experiment lasted 27–35 min, with 7 min required for the acoustic presentation of the 20-word lists. Twenty additional min were required by TMS procedures.

Procedures of TMS, Navigation, and Targeting

rTMS was delivered using a biphasic MagstimSuperRapid stimulator (Magstim Co., United Kingdom), connected to an eight-shaped coil (diameter of each wing = 7 cm). Before the start of the task, single TMS pulses were delivered to the hand area of the left primary motor cortex to establish the individual excitability threshold measured from the right first dorsal interosseous muscle. Then, the stimulator output was tuned down to an intensity corresponding to the 90% of the individual threshold (mean intensity of the maximal stimulator output used = 49.8, SD = 6.6%).

The rTMS train (500 msec at 10 Hz) started 100 msec before the offset of each presented word. Such a timing of TMS trigger corresponded to the timing of the maximal detrimental effect on memory, as previously demonstrated by Rossi, Innocenti, et al. (2011). The noise of the coil click did not affect the quality of word perception, as demonstrated by the similarity between the accuracy indexes measured during baseline (i.e., no rTMS) and during rTMS to the vertex. The combination of intensity, length of stimulation, intertrain intervals, and number of trains fit well with the safety guidelines of rTMS applications (Rossi, Hallett, Rossini, & Pascual-Leone, 2009). The experiment was preceded by a 5-min training phase to familiarize participants both with the task and the scalp sensation induced by rTMS.

Stimulation sites for TMS were identified on each participant's scalp using a TMS-magnetic resonance imaging coregistration system (SofTaxic optically tracked by EMS, Siena, Italy). This navigated stimulation system, fully described in a previous article (Feurra et al., 2011), was used throughout the experiment. The system allows for the exact repositioning of the TMS coil in real time within and across experimental sessions, with a tolerance of 2–3 mm for each of the Cartesian coordinates. Moreover, it minimizes the variability of TMS-induced electric fields directly measured within a scalp model (Cincotta et al., 2010). Talairach coordinates of cortical sites were automatically estimated by the Navigator System, on the basis of an MRI-constructed stereotaxic template.

Coordinates (mm) for the left DLPFC ($x = -31, y = 44, z = 25$) corresponded to the left DLPFC, Brodmann's area 9, according to previous neuroimaging results (Wagner, Maril, Bjork, & Schacter, 2001). The left IPL coordinates ($x = -42, y = -54, z = 42$) corresponded to the left supramarginal gyrus (Brodmann's area 40; O'Connor, Han, & Dobbins, 2010), according to previous neuroimaging studies investigating phonological WM (Paulesu, Frith, & Frackowiak, 1993) and recency processing (Talmi et al., 2005). The vertex stimulation site was defined as a point midway between the inion and the nasion and equally distant from the left and right intertragal notches. Because this region is mechanistically excluded by episodic memory processes, it was considered as a control site for possible unspecific or arousal effects of rTMS induced by somatosensory and acoustic stimulations.

Data Analysis

Two experimenters independently took note of the remembered words and of the serial position in which they had been acoustically presented within each list. Any occasional intrusion (i.e., words incorrectly rated as listened by participants) was also noted. However, they are not reported because they rarely occurred. The nature of the free recall task did not contemplate any RT.

For each participant, the 20-word lists were grouped into five clusters: primacy cluster (serial positions from 1 to 4), three middle clusters (5–8, 9–12, and 13–16), and recency cluster (17–20). For each participant, behavioral performance was separately evaluated by each list and experimental condition through accuracy measures (number of recalled items). The dependent variable was the percentage of words correctly recalled as a function of word presentation order. The mean percentage was calculated for each cluster. The collected data were entered in a two-way repeated-measures ANOVA with TMS Site of Stimulation (four levels: baseline, rTMS of the left DLPFC, left IPL, and vertex) and Serial Position Cluster (five levels: 1–4, 5–8, 9–12, 13–16, and 17–20) as within-subject factors. To correct violations of the sphericity assumption, Greenhouse–Geisser corrections were applied when necessary. Post hoc tests were performed by Bonferroni test. For all analyses, significance was set at $p < .05$.

RESULTS

Participants tolerated well the rTMS protocol, and no side effects occurred. All participants completed the study. Behavioral performances in the free recall task after rTMS to the left DLPFC and to the left IPL were compared with those obtained in a baseline condition (without rTMS at encoding). In addition, rTMS was also delivered to the vertex as a control condition to check for the site specificity of interference effects.

The serial position effect (summarized in Figure 1) was analyzed with respect to the five clusters obtained by dividing the 20-word list as follows: serial positions 1–4 (considered as primacy cluster), 5–8, 9–12, 13–16 (considered as middle clusters), and 17–20 (considered as recency cluster). A two-way repeated-measures ANOVA on the mean percentage of words correctly recalled as a function of order presentation showed a main effect of Serial Position Cluster ($F(4, 12) = 119.388$, $p < .001$) and of rTMS Site of Stimulation ($F(3, 12) = 8.749$, $p < .001$). The interaction between these two factors was also significant ($F(4, 48) = 5.843$, $p < .001$). As expected,

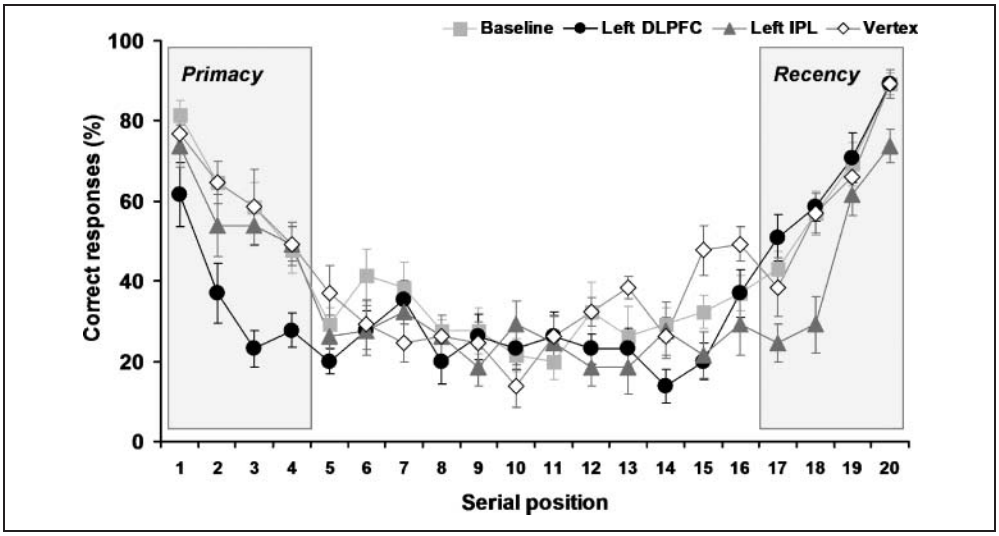

Figure 1. The "U-shaped serial position curve" of the 20-word list during the immediate free recall task. Basal condition (no rTMS, gray squares) during rTMS of the left DLPFC (black circles), rTMS of the vertex (empty diamond), and rTMS of the left IPL (gray triangles). Note that the left DLPFC stimulation decreased primacy but not recency, whereas the left IPL stimulation decreased recency, leaving unaltered primacy. These effects are even more evident if the first and last two items (i.e., those likely better memorized, thereby less susceptible to rTMS interference) are not considered. Statistics for the whole "U-shaped serial position curve" are in the text.

participants were generally more accurate in recalling words presented at the beginning and at the end of the list (Clusters 1–4 and 17–20, respectively). Post hoc comparisons (Bonferroni corrected) revealed that, for the baseline condition (no rTMS during the encoding), the percentage of recalled words was significantly higher for Clusters 1–4 (primacy) and 17–20 (recency) compared with all other clusters in the middle of the curve ($p < .001$, for all comparisons). The same pattern was observed for the control condition (rTMS of the vertex; $p < .001$, for all comparisons).

For the rTMS to the left DLPFC condition, the primacy effect was still present but strongly reduced (accuracy for Cluster 1–4 was significantly higher than Clusters 9–12 and 13–16; $p = .027$ and $p = .011$, respectively), whereas the recency effect was completely preserved. The accuracy for Cluster 17–20 was significantly higher compared with Cluster 1–4 and with all other clusters in the middle of the curve ($p < .001$, for all comparisons).

An opposite pattern of results was observed for the rTMS to the left IPL. The recency effect was reduced (the accuracy for Cluster 17–20 was significantly lower with respect to Clusters 5–8, 9–12, and 13–16; $p < .001$, for all comparisons), whereas the primacy effect was preserved (accuracy for Cluster 1–4 was significantly higher than Clusters 5–8, 9–12, and 13–16; $p < .001$, for all comparisons).

The double dissociation between rTMS-induced effects on the free recall performance after interference with the left DLPFC versus the left IPL was further confirmed by additional post hoc comparisons. Specifically, for Cluster 1–4, the number of words recalled was significantly lower when rTMS was applied to the left DLPFC with respect to the other experimental conditions ($p < .001$, for all comparisons; Figure 2). On the contrary, specifically for Cluster 17–20, the behavioral performance was significantly lower when rTMS was applied to the left IPL with respect to the other experimental conditions ($p < .001$,

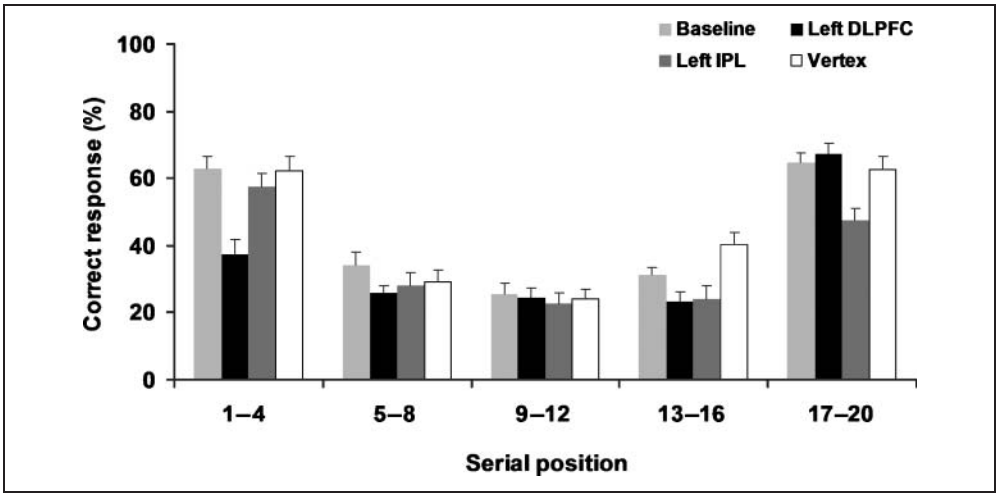

Figure 2. Percentage of correct responses expressed as clusters, according to each experimental condition. Primacy (Cluster 1–4) and recency (Cluster 16–20) clusters show the best performances. The accuracy in primacy and recency is selectively worsened by rTMS applied, respectively, in encoding on the left DLPFC (black bars) and on the IPL (dark gray bar). Differences across conditions in the other clusters are not significant (statistics is in the text).

$p < .001$, and $p = .003$, respectively; Figure 2). No significant difference across conditions emerged for the remaining clusters.

DISCUSSION

We showed a clear-cut double dissociation concerning the detrimental effects on memorization abilities induced by rTMS. Stimulation of the left DLPFC selectively affected the primacy effect, sparing the encoding of the last presented words; conversely, stimulation of the left IPL selectively affected the recency effect, leaving unaltered the encoding of early presented words. These effects were interindividually consistent and regionally specific, because rTMS applied to a control brain region not involved in memory processes (i.e., the vertex) did not impact on memorization abilities (Figure 1). At the descriptive level, it is worth noting that the impact of rTMS on memorization abilities was even greater if the very first and last two items of the serial position curve were not considered (see Figure 1). This would imply that rTMS interference is more likely to occur when the strength of the memory trace is weakening down (i.e., if the trace is stronger, as for the very first and last items, then rTMS interference is less effective), according to a task dependency of TMS effects. However, such a possible task (and state) dependency of rTMS effects on primacy and recency mechanisms should be better addressed in future studies combining simultaneous rTMS with EEG/fMR recordings, as it has been done for WM operations (Johnson, Kundu, Casali, & Postle, 2012). According to the latter study, such an approach may definitely help to conclude whether the degree of engagement of the target region in the primacy/recency memory task determines the degree of rTMS-induced changes in the functional networks implicated in task performance.

The primacy/recency double dissociation induced by rTMS at prefrontal/parietal sites provides the first causal evidence for the existence of selective cortical mechanisms involved in semantic and phonological encoding of incoming verbal information in healthy humans. Indeed, previous neuroimaging studies provided some support to the dual storage model (Fletcher & Henson, 2001), since successful recall of early presented probes was associated with activation of the left hippocampal region (Karlsgodt, Shirinyan, van Erp, Cohen, & Cannon, 2005)—a finding that appears to be selective for primacy but not for recency retrieval (Talmi et al., 2005; Wagner et al., 2001; Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000; Schacter & Wagner, 1999). In contrast, retrieval of recency probes, which are temporarily stored, has been associated with an increased activation of neocortical brain regions, such as the superior temporal sulcus (Ranganath & D'Esposito, 2005; Zhang et al., 2003; Konishi et al., 2002) and the inferior parietal lobe (Buchsbaum, Padmanabhan, & Berman, 2011; Buchsbaum, Ye, & D'Esposito, 2011; Greve et al., 2010; Buchsbaum & D'Esposito, 2009; Nee & Jonides, 2008; Dudukovic & Wagner, 2007; Talmi et al., 2005). Cabeza, Dolcos, Graham, and Nyberg (2002), however, reported a large fronto-parieto-cerebellar overlap of the areas involved in episodic recall (ER) and WM. The latter study showed both common and specific subregion activations within the pFC. Left dorsolateral prefrontal areas were activated by both ER and WM, whereas bilateral anterior and ventrolateral areas were more active during ER than during WM. Left posterior/ventral (Broca's area) and bilateral posterior/dorsal areas were more active during WM than during ER. In addition, hippocampal and parahippocampal regions were activated not only for ER but also for WM.

The detrimental impact of DLPFC interference on long-term encoding is compatible with the supervising role that the left DLPFC maintains in episodic encoding throughout the life span (Rossi et al., 2004), as well as on a key functional role for the primacy effect. This could be expected, taking into account that the left DLPFC, which is known to exert a top–down hierarchical control on medial-temporal lobe neural structures, including the hippocampus, plays a crucial role in semantic encoding (Rossi, Innocenti, et al., 2011; Gagnon, Blanchet, Grondin, & Schneider, 2010; Innocenti et al., 2010; Turriziani, Smirni, Oliveri, Semenza, & Cipolotti, 2010; Rossi et al., 2001, 2004, 2006; Floel et al., 2004; Rami et al., 2003; Sandrini et al., 2003).

Current rTMS results in healthy participants fit nicely with previous neuropsychological studies in patients with brain lesions, which showed double dissociations between post-lesional memory performance for early and late presented items. Amnesic patients had preserved recency but abolished primacy effect (Milner, 1974; Baddeley & Warrington, 1973; Warrington & Shallice, 1969). Patient K. F. (Shallice & Warrington, 1970), following a left occipito-parietal lesion, had a recency effect limited to a single item, in spite of preserved long-term learning abilities. Patient P. V. (Vallar & Papagano, 1986), who had a selective deficit of short-term auditory/verbal memory with intact long-term memorization abilities, showed an abolition of the recency effect with unaltered primacy. It may be noted, however, that brain lesions in the chronic phase are usually followed by plastic reorganization mechanisms, which may promote behavioral adaptations; this may preclude generalization of results to healthy brains. In contrast, the present direct demonstration of a "double route" for encoding in healthy humans is entirely original and represents a striking example of the causal utility of rTMS in cognitive neuroscience.

The present findings are compatible with the hypothesis that separate mechanisms are responsible for short-term (recency) and long-term (primacy) encoding. Short-term encoding, which would explain the recency effect, could have a direct access from the IPL region through phonological encoding of the acoustically processed items. A direct link between the left IPL activity and the primary

auditory input buffer has been already postulated (Zhang et al., 2003). Evidence from neuropsychological studies (Baldo & Dronkers, 2006) and imaging data (Hickok & Poeppel, 2007) converges in assigning a crucial role to this region in phonological processing. An alternative interpretation in terms of interference with attentional mechanisms (Nee & Jonides, 2008) seems unlikely, as it would predict a selective vulnerability of the most recent item(s), which was not observed in our study. Conversely, at the experimental debriefing, our participants were generally well confident that the first remembered words were the "last listened" among the presented list.

According to the multiple store model, STS and LTS systems, despite partly independent, might be integrated, thanks to the episodic buffer (Baddeley, 2000), thereby becoming functionally linked to each other. The results, however, are also compatible with a unitary memory store, which works with parallel, separate encoding mechanisms. A reconciling hypothesis could be that both short- and long-term encoding are simultaneously active during elaboration of the incoming information. Then, to avoid the overload of the capacity-constrained memory system, only certain probes will be maintained available for immediate free recall, whereas others are discarded. However, the factors influencing the chance of a probe to undergo "consolidation" in the memory trace rather than oblivion have not been addressed in this study.

The hypothesis of the "bimodal encoding" is supported by the overt double dissociation emerged from our study, which strongly points against the possibility of a unique "entry door" into memory system. If this were the case, indeed, both primacy and recency mechanisms should have been affected in the same manner, irrespective of the stimulation site.

In conclusion, the present findings in healthy humans concur with patient data in falsifying the serial model of memorization, which implies a mandatory passage through STS for items to reach LTS. Moreover, these findings are fully compatible with an alternative model, which entails multiple encoding mechanisms, with parallel privileged accesses to STM and LTM. Within the WM model, the privileged role of the STM store is the shallow encoding of information, which, in the case of language, is required for phonological learning. On the other hand, meaningful information, such as in the case of real words, can make use of a direct access to the LTM store via deep encoding. Whereas the crucial role of the IPL as the neural basis of STM encoding and retention was already clearly highlighted by clinical data, the present data elucidate the crucial role of the middle frontal gyrus in deep semantic encoding, in agreement with previous imaging and rTMS data.

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