Topological Self-Organization and Prediction Learning Support Both Action and Lexical Chains in the Brain

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Abstract

A growing body of evidence in cognitive psychology and neuroscience suggests a deep interconnection between sensory-motor and language systems in the brain. Based on recent neurophysiological findings on the anatomo-functional organization of the fronto-parietal network, we present a computational model showing that language processing may have reused or co-developed organizing principles, functionality, and learning mechanisms typical of premotor circuit. The proposed model combines principles of Hebbian topological self-organization and prediction learning. Trained on sequences of either motor or linguistic units, the network develops independent neuronal chains, formed by dedicated nodes encoding only context-specific stimuli. Moreover, neurons responding to the same stimulus or class of stimuli tend to cluster together to form topologically connected areas similar to those observed in the brain cortex. Simulations support a unitary explanatory framework reconciling neurophysiological motor data with established behavioral evidence on lexical acquisition, access, and recall.

Keywords: Motor chains; Lexical chains; Serial working memory; Computational modeling; Self-organizing maps; Somatotopic organization; Prediction

1. Introduction

The classical view that language comprehension and production are the result of cognitive operations on abstract amodal symbols is increasingly challenged by evidence that language processing exploits, at least partially, the same neural systems supporting perception, action, and emotion (Barsalou, 2008; Glenberg & Kaschak, 2002; Pulvermüller & Fadiga, 2010). Somatotopic activations of the premotor and parietal cortices have been

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experimentally observed in connection with both action performance and linguistic tasks such as reading and listening to verbal expression of actions (Pulvermuller, 2005; Rizzolatti, Cappa, & Perani, 2005; Tettamanti et al., 2005). In this article, we intend to explore a somewhat complementary and more functional view on this relationship. We offer a computational analysis and a conceptual meta-analysis of experimental results supporting the hypothesis that learning/processing mechanisms for both motor and linguistic structures in the brain are functionally based on a common pool of principles governing topological self-organization, prediction-driven learning, and the dynamic between short-term and long-term memory processes. These mechanisms develop neuronal "chains" consisting of dedicated context-responsive nodes, organized into topological clusters of type-responsive nodes. This may shed light on structural similarities observed between action and language, such as hierarchical organization, compositionality and chunking, to suggest that (a) phylogenetically, language processing could have reused (or co-developed) organizing principles, processing, and learning mechanisms typical of motor areas (Rizzolatti & Arbib, 1998); (b) ontogenetically, knowledge of serial order through motor exploration can bootstrap language acquisition (Dominey & Ramus, 2000).

2. Action encoding in the brain

The encoding of motor actions in the brain is achieved by a network that comprises various areas elaborating information at different levels of detail. In decreasing order of abstractness, one can find the parietal lobe, the premotor cortex, and the primary motor cortex. The parietal cortex is traditionally considered an association area that integrates different sensory modalities, encodes motor acts, and provides them with specific sensory information. Recent experiments (Fogassi et al., 2005; Gallese, Fadiga, Fogassi, & Rizzolatti, 2002; Rozzi, Ferrari, Bonini, Rizzolatti, & Fogassi, 2008) have studied the functional and cytoarchitectonic properties of this area characterizing its somatosensory, visual, and motor responses. These studies show that the inferior parietal lobule (IPL) contains a rich variety of neurons responsive to distinct sensory stimuli and discharging in association with different types of actions such as reaching, grasping, and bringing to the mouth, both when executed and when observed. Additionally, motor responses are somatotopically organized with the mouth represented more rostrally (in PF), then the hand (in PFG) and the arm more caudally (in PG) with a certain degree of overlap between adjacent representations (see Fig. 1). In each subdivision, the motor activity is associated with correlated somatosensory and visual responses.

Another key feature of the recorded motor neurons in IPL is that their response is strongly modulated by the intended goal of the whole action sequence (Chersi, Ferrari, & Fogassi, 2011; Fogassi et al., 2005). It has been hypothesized that this brain area presents a highly structured organization, where pools of neurons encoding subsequent motor acts leading to a specific goal are connected in goal-driven chains (see Fig. 2). According to this view, the execution and the recognition of actions are achieved through the propagation of activity within the appropriate chains (thus resulting in the firing of only specific
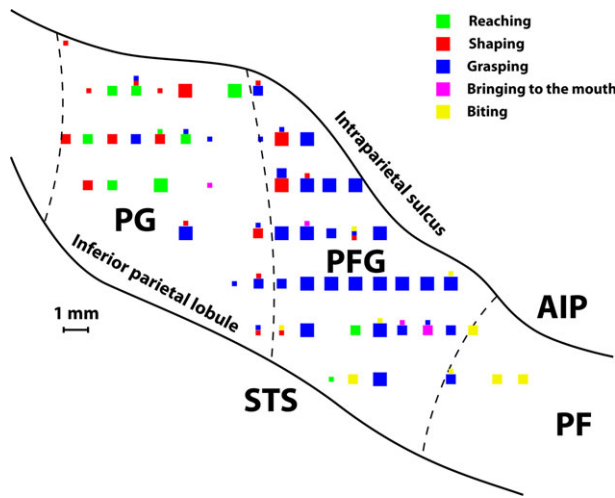
Fig. 1. Functional organization of the parietal cortex of a monkey. Dots of different colors represent different motors acts. The size indicates the local percentage of neurons encoding that specific act (modified from Rozzi et al., 2008).
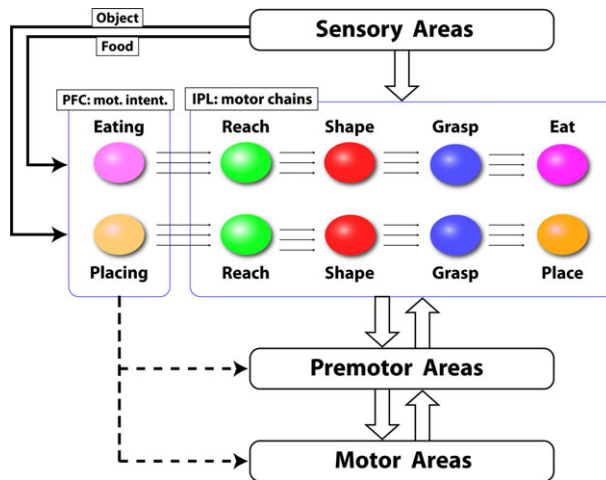

Fig. 2. Simplified representation of the "Chain Model" (Chersi et al., 2011). Colored ellipses represent subpopulations of neurons encoding specific motor acts in the parietal cortex (IPL) or intentions in the prefrontal cortex (PFC). Arrows indicate the connections between different subpopulations (for the sake of clarity, not all connections have been indicated). Sensory areas, which comprise the superior temporal sulcus, the inferior temporal, somatosensory, and auditory areas, provide information about the ongoing action, while premotor and motor areas convert signals into motor commands.

neurons). Furthermore, neurons in one chain are not interchangeable with those of other chains even if they code the same motor act. The hypothesis is justified by the dense interconnection between IPL and the dorsolateral prefrontal cortex, which is generally assumed to play the role of maintenance and goal-directed control of sequential

representations (Goldman-Rakic, 1987; Petrides, Alivisatos, Meyer, & Evans, 1993). Although in this model prefrontal cortex (PFC) has a modulatory role only for IPL, the anatomical connections between PFC and premotor/motor cortexes (Guye et al., 2003; Young, Scannell, & Burns, 1995) make room for the hypothesis that similar loops exist at multiple levels of the brain motor hierarchy.

3. Lexical encoding in the human brain

Diffusion tensor magnetic resonance imaging data of the left hemisphere of human brain have provided neuroanatomical evidence of a bidirectional perisylvian pathway from the superior temporal gyrus (STG, or Wernicke's area) to Broca's area through IPL (Catani, Jones, & ffytche, 2005). The network defines the neuro-cognitive substrate to the retention of sequences of linguistic units and orosensory goals for their vocalization in working memory (Gathercole & Baddeley, 1989; Papagno, Valentine, & Baddeley, 1991). Since Baddeley's pioneering work, working memory was assumed to include a volatile phonological store in the supramarginal gyrus (SMG) and a "phonological loop" mechanism refreshing the store's auditory content through subvocal rehearsal (Awh, Smith, & Jonides, 1995; Frackowiak, 1994; Paulesu, Frith, & Frackowiak, 1993). More recently, several researchers (e.g., D'Esposito, 2007; Wilson, 2001) have suggested a view of verbal working memory as a dynamic form of sensory-motor integration. Accordingly, the storage component should be located in auditory-responsive fields in STG (Hickok & Poeppel, 2004; Shalom & Poeppel, 2008), with the functional connectivity of the posterior segment in the arcuate fasciculus (from STG to SMG) providing a bidirectional mapping: (a) auditory-to-motor mappings support verbatim repetition of heard speech, and (b) motor-to-auditory mappings are used to activate auditory representations of speech through controlled articulatory rehearsal in frontal circuits. Under this view, integration of auditory-motor circuits ensures maintenance/control of transient activation of long-term memory structures in the absence of external stimuli.

The hypothesis establishes a close connection between lexical processing and working memory in terms of the anatomical arrangement of the neural networks involved. Linguistic units that are frequently sequenced together are consolidated in Wernicke's area, where they are accessed and executed as highly automatized routines. This increases fluency and accounts for the memory effect known as "chunking" (Cowan, 2000; Miller, 1956). Finally, the view establishes an interesting parallelism with the encoding and execution of motor sequences as chains of dedicated and topologically organized neurons (Chersi et al., 2011). Computational modeling of self-organizing memories can bridge evidence in both domains.

4. Computational modeling

Topological models of the mental lexicon based on temporal self-organizing maps (TSOMs; Koutnik, 2007; Ferro, Ognibene, Pezzulo, & Pirrelli, 2010) can mimic the

spatial and temporal organization of memory structures supporting the processing of symbolic sequences (Ferro, Marzi, & Pirrelli, 2011; Marzi, Ferro, & Pirrelli, 2012; Pirrelli, Ferro, & Calderone, 2011). Through repeated exposure to recurrent word forms, TSOMs develop chains of discharging nodes (Fig. 3). In some cases, node chains are arranged in rooted hierarchies, where each node can be reached by one connection only ("word tries": Fredkin, 1960). In other cases, the chains allow the same node to be reached by multiple connections ("word graphs"). Word tries are entrenched, dedicated memory structures, whereby partially overlapping strings activate distinct nodes. Word graphs, conversely, allow for shared substrings to activate identical nodes. These competing memory structures emerge from topological self-organization, whereby nodes responding to the same input symbol tend to cluster in topologically connected regions of the map, similar to those observed in cortical areas involved in the classification of sensory data (Aflalo & Graziano, 2006). The topological distance between any two nodes thus reflects their degree of specialization to stimuli in the input space and is a function of frequency distributions in the training data, degree of structural redundancy, and learning epochs.

TSOMs provide a suitable computational framework to test fundamental mechanisms underpinning serial cognition and self-organization. In what follows, we show how different frequency distributions of training data affect the developmental trajectory of a TSOM through the combined interplay of competition and familiarization, and we relate the observed dynamics to available neurophysiological and behavioral evidence. This may provide an explanation of "what" is observed and "where" in the brain, in terms of "how" it comes about.

5. The architecture

TSOMs augment Kohonen's self-organizing maps (SOMs; Kohonen, 2001) with weighted re-entrant temporal connections (Fig. 4). Nodes on the input layer are fully connected with the map activated at the current time t, or (t) *map*, to which temporal connections reverberate the map's activation pattern at the immediately preceding time tick, buffered on the $(t−1)$ *map*. When an input stimulus is presented, (t) *map* nodes are activated synchronously, with the most highly activated node, or best matching unit (BMU (t)), being selected as the winner. We call *pattern recoding* the transformation of an input vector into a map activation pattern. Activation of node n_i at time t is the sum of two values. The first value says how close input connection weights of node n_i are to the current

Fig. 3. Node chains in a TSOM for the Italian forms *vediamo* ("we see") and *crediamo* ("we believe"). Dedicated chains are reminiscent of word tries (left) and interlocked chains of word graphs (right). In word graph-like chains, connections to competing, less highly activated nodes (dotted arcs) are not severed.

input representation. The second value says how predictable the current input is on the basis of the activation pattern on the *(t−1) map*. In presenting a sequence of stimuli, activation patterns of the *(t−1) map* are accumulated in the Σ *map*, where the input sequence is temporarily stored as a short-term *integrated activation pattern*.

TSOMs can be trained on sets of input sequences. During training, at each time *t*, *BMU(t)* adjusts its weights on both input connections and temporal re-entrant connections, and propagates adjusted values to neighboring nodes. Adjustment of input connections makes weights closer to input vector values. Adjustment of temporal connections, on the other hand, potentiates the strength of association from *BMU(t−1)* to *BMU(t)* (and neighboring nodes) and depresses the strength of association from all other nodes on the *(t−1) map* to *BMU(t)* (and neighboring nodes). This encodes the network probabilistic expectations over sequences of symbols, thereby developing dedicated chains of nodes reminiscent of word tries (Fig. 3, left).

6. Testing motor and lexical chains

After training, weights on both input connections and re-entrant temporal connections are frozen and the map is tested on two tasks: *pattern recoding* and *pattern recall*. Accuracy in pattern recoding measures the vector distance between the current input vector and the input connection weights of the corresponding *BMU*. We count a hit, if the vector distance is below an error threshold (10% of max error). A sequence is recoded
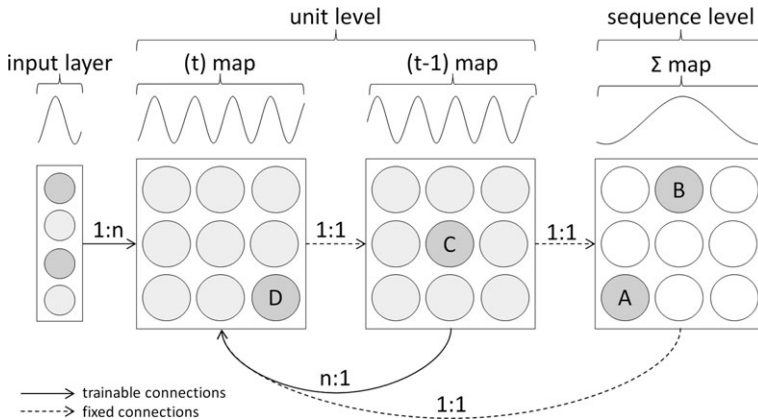

Fig. 4. A TSOM-based lexical architecture. Activation patterns over consecutive time ticks (*pattern recoding*) are buffered into a Σ *map*, where a whole input sequence is represented topologically (*integrated activation pattern*). Re-entrant temporal connections are eventually used to recover the appropriate order of input stimuli from the Σ *map* (*pattern recall*). The figure shows patterns of activation upon presentation of the character "D" in the string "ABCD." Labels indicate which *BMU* is activated in association with a particular symbol. Sinusoids on top of each map represent activation persistence over time, with activation on the Σ *map* spanning several time ticks.

accurately if all its units are recoded accurately. On pattern recall, the map reinstates an input sequence from its short-term integrated activation pattern on the Σ *map*, based on temporal connections only (i.e., with no external information being provided by the input layer: Fig. 4). A stimulus is accurately recalled if the vector distance between the stimulus input vector and the input connection weights of the reinstated *BMU* is below threshold. A sequence is recalled accurately if all its units are recalled accurately. In our experiments, the architecture is trained to memorize patterns representing sequences of either motor acts (experiment 1) or letters (experiment 2). During training, multiple instances of an input sequence are shown to the map, according to the frequency distribution associated with the sequence. Hereafter, we will speak of *types* to refer to sequences, and of *tokens* to indicate sequence instances.

6.1. Experiment 1

6.1.1. Method
A training set of partially overlapping goal-directed action chains was obtained by combining 19 distinct motor acts in sequences of different length. Each sequence started with a goal, followed by the motor acts taken to attain the goal. For example, the motor sequence "reaching, grasping and taking food for eating" is encoded as "ToEat, Reach, Grasp, Take," with each item in the sequence being input to the map as an independent stimulus at time *t*. TSOMs of different size (from 25 up to 225 nodes) were trained on motor sequences for 100 learning epochs each. To investigate the interplay between frequency, competition, and familiarization, experiments were run on two different frequency distributions over the same training set: a uniform distribution (with sequences presented 10 times each) and a skewed distribution (with some sequences being presented 50 times more frequently than others). For each different combination of map size and training data distributions, we repeated the experiment 20 times.

6.1.2. Results
Trained maps (Fig. 5) were tested on two tasks: pattern recoding and pattern recall (Fig. 6). Test stimuli consisted of the same motor sequences used for training. We also looked at the topological distance of *BMU* chains activated by the same input subsequence through both learning epochs and maps of growing size (Fig. 7).

6.2. Experiment 2

6.2.1. Method
A non-defective Italian verb can be inflected for over 50 different combinations (or paradigm cells) of morpho-syntactic features such as tense, person, number, and mood. We selected 13 Italian verbs by decreasing values of frequency distribution in a newspapers corpus and picked up 15 inflected forms of each verb from the same set of paradigm cells. The resulting 195 forms were encoded as strings of letters preceded by a blank
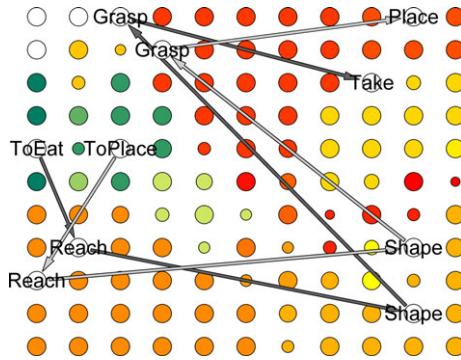
Fig. 5. Activation chains of BMUs triggered by "ToEat, Reach, Shape, Grasp, Take" and "ToPlace, Reach, Shape, Grasp, Place" on a 11×11 TSOM trained on skewed distributions. Different nodes selectively respond to "Reach, Shape, Grasp" when the sequence is seen in the two action patterns.
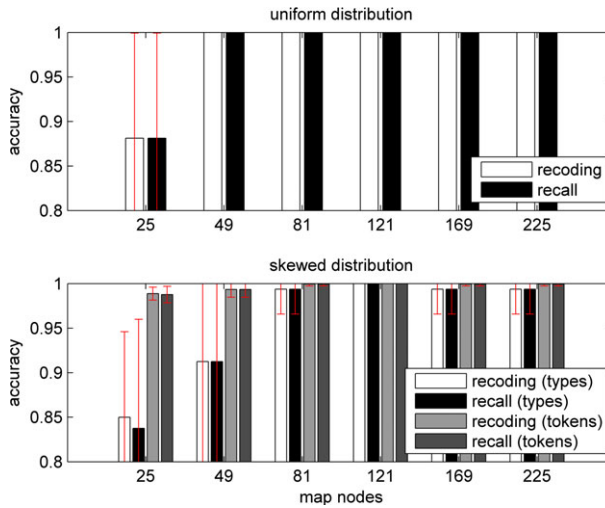

Fig. 6. Accuracy on pattern recoding and recall for maps of different size, trained on uniform (top) and skewed (bottom) distributions of input data. Skewed distributions make low-frequency data more difficult to recall, with high-frequency patterns strongly competing for dedicated chains. Scores are averaged across 20 repetitions of the same experiment.

character to form the training set. Each string was input to a TSOM one character at a time. TSOMs of different size (from 100 up to 1600) were trained over 100 epochs. To analyze the influence of token/type frequency in training, experiments were run on two different distributions: the real corpus distribution of 195 inflected forms (skewed distribution) and a uniform distribution. Each combination of map size and training regime was repeated five times.
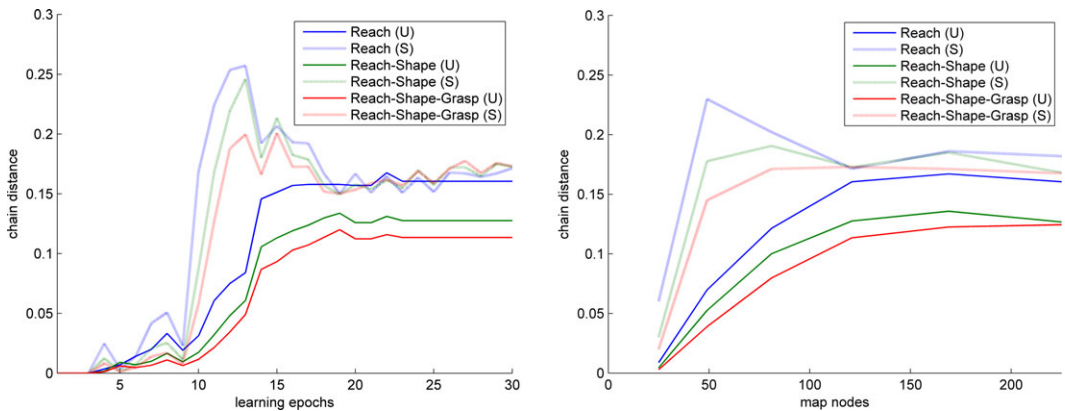
Fig. 7. Left: internode distance for "Reach-Shape-Grasp" in maps trained on uniform ("U," solid lines) and skewed ("S," shaded lines) distributions of motor sequences over the first 30 learning epochs. Goal-specific acts recruit distinct nodes in their order of appearance in the sequence. High-frequency sequences are shown to recruit dedicated chains earlier than uniformly distributed sequences. Distance values are averaged across 20 repetitions. Right: internode distance for "Reach-Shape-Grasp" in maps of different size trained on uniform and skewed sequence distributions. Smaller maps are more sensitive to competition effects prompted by skewed distributions. Values are averaged across 20 repetitions for each map size. Distances are normalized with respect to the map's diagonal.

6.2.2. Results

The topological organization of trained maps was monitored through learning epochs and probed on two tasks: word recoding and word recall. Test stimuli consisted of the same 195 forms used for training. Results are reported in Fig. 8 (right). We also measured the topological distance between nodes that discharge upon presentation of an infinitival ending in a target word (e.g., *ere* in *avere* "to have"), and nodes that discharge during presentation of the same ending in all other test words (Fig. 9, top). Finally, the same distance was measured within two groups of verbs, {*avere*, *credere*, *essere*} and {*tenere*, *vedere*, *volere*}, in the two conditions of uniform and skewed distribution (Fig. 9, bottom).

7. General discussion

Our simulations were intended to establish a connection between motor and lexical tasks, serial working memory, and sequential processing. Evidence of different pools of neurons being activated by goal-specific motor acts emerged as the result of a process of adaptive specialization of long-term memory circuits for serial cognition (Experiment 1). In TSOMs, the process is accounted for as the outcome of a dynamic trade-off between a predictive bias for dedicated chains and available memory resources. When a map is trained on several motor sequences, recoded sequences compete for map space as a function of their distribution. Fig. 7 (left) shows the average topological distance between
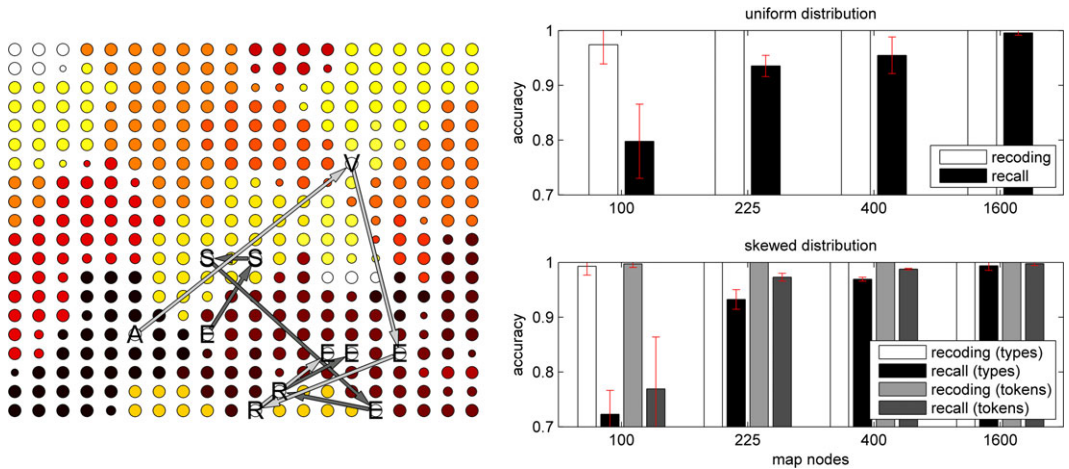
Fig. 8. Left: A 20 × 20 TSOM trained on a skewed distribution of Italian verb forms. Nodes with different colors are sensitive to different alphabetical symbols with accuracy proportional to dot size. Arrows connect sequentially activated *BMU*s (activation chains) triggered by the Italian infinitival forms *essere* ("to be") and *avere* ("to have"). Note that distinct nodes discharge in association with the same ending *–ere*. Right: Accuracy in word recoding and recall on maps of increasing size, trained on uniform and skewed distributions. Skewed distributions make low-frequency forms harder to recall from smaller maps. Scores are averaged across five instances of the same experiment.

*BMU*s for "Reach," "Shape," and "Grasp" in the sequences "ToEat, Reach, Shape, Grasp, Take" and "ToPlace, Reach, Shape, Grasp, Place," through the first 30 learning epochs. The two sequences activate the same nodes at early learning epochs, to gradually recruit more dedicated nodes as learning progresses. In the end, fully distinct chains develop. High-frequency sequences demonstrably develop dedicated chains earlier than low-frequency sequences. This is conducive to better recall, particularly in small-size maps where competition for space is stronger and goal-specific actions are recoded comparatively further apart than in larger maps (Fig. 7, right). All of this is compatible with the organization of monkeys' parietal and premotor cortex (Bonini et al., 2010, 2011; Rozzi et al., 2008) where topological constraints reflect proximity of actions in a behavioral space (Aflalo & Graziano, 2006). Furthermore, it is in good agreement with the hypothesis that the monkeys' action repertoire is structured into dedicated chains, including specialized neural units (Chersi et al., 2011; Fogassi et al., 2005), as confirmed by a microanalysis of levels of activation of discharging nodes. Table 1 shows the number of nodes that are more highly activated by "Grasp ToEat" (ToEat > ToPlace"), nodes that are more highly activated by "Grasp ToPlace" (ToPlace > ToEat"), and nodes that are equally activated by "Grasp" in the two contexts (ToEat = ToPlace), for both uniform and skewed distributions of the two goals. In the skewed distribution condition, the uneven allocation of goal-specific nodes ("ToEat ≠ ToPlace") shows that the number of goal-specific nodes can be a function of how often a motor act is practiced in connection with a particular goal. Our data are consistent with data reported by Fogassi et al. (2005),
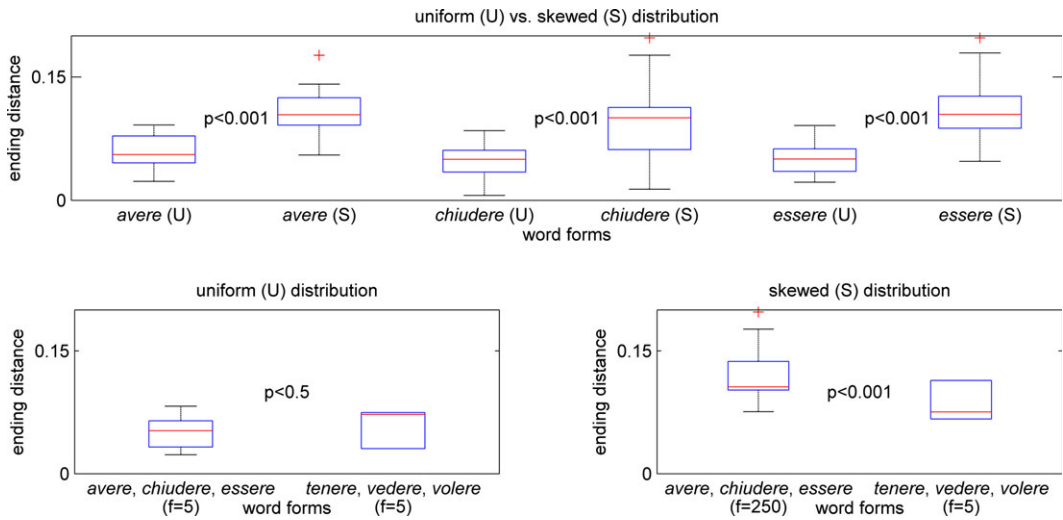
Fig. 9. Top panel: Box plots of topological distances between map nodes discharging on Italian infinitival endings presented with uniform ("U") and skewed ("S") distributions. The distance is significantly larger ($p < 0.001$) for high-frequency verb forms than for the same forms in a uniformly distributed training set. Bottom panels: Average distances between nodes discharging on infinitival endings within two groups of verbs. Within-group distances differ significantly between low-frequency and high-frequency verbs (right), and they do not differ when the same verbs are uniformly distributed (left). (Distances are averaged across five instances of the same experiment, $f(x)$ indicates form frequency.)

and they support the suggestion that brain areas in IPL provide the opportunity of using both general (goal-aspecific) and goal-specific information simultaneously, with frequent motor chains being compiled into a sort of "lexicon" of routinized behavioral patterns.

The word lexicon is organized according to similar principles. Converging empirical findings suggest that surface word relations constitute a fundamental domain of lexical competence, as shown by the interplay between form frequency, family frequency and family size effects in both inflectional and derivational word families. It is a well-established fact that the token frequency of an inflected form facilitates lexical access and correlates negatively with response latencies in visual lexical decision (Taft & Forster, 1975; Whaley, 1978). More recently, token frequency effects are shown to interact with family frequency. The more frequent an inflected form is relative to its base (e.g., *walked* vs. *walk*), the more salient the whole is relative to its parts (Hay & Baayen, 2005). A more uniform frequency distribution over members of the same inflectional paradigm makes them more readily accessible (Baayen, Feldman, & Schreuder, 2006; Moscoso del Prado Martín, Bertram, Häikiö, Schreuder, & Baayen, 2004), favoring a better allocation of memory resources. Our results are in keeping with this evidence. Despite ubiquitous patterns of redundant morphological structure in training data, and contrary to considerations of storage economy, TSOMs develop dedicated memory chains (word tries) to process high-frequency inflected forms. In Fig. 9 above, nodes that discharge in association with endings in high-frequency forms are significantly more distant from nodes discharging

Table 1
Allocation of discharging nodes for "Grasp ToEat" and "Grasp ToPlace" in two maps trained on a uniform (left column) and a skewed distribution (right column) of the sequences "ToEat, Reach, Shape, Grasp, Take" and "ToPlace, Reach, Shape, Grasp, Place." Percentages in squared brackets, from Fogassi et al. (2005), are reported for comparison. Results are averaged over 20 instances of each map. See text for further details

No. Chains	freq (To Eat) = 55; freq (To Place) = 55		freq (To Eat) = 100; freq (To Place) = 10	
		$p < 1$		$p < 0.00001$
No. nodes	To Eat > To Place:	15.8 (45.3%)	To Eat > To Place: [72.6%]	12.6 (88.1%)
	To Place > To Eat:	19.1 (54.7%)	To Place > To Eat: [27.4%]	1.7 (11.9%)
	To Eat ≠ To Place:	34.9 (40.1%)	To Eat ≠ To Place: [64.2%]	14.3 (28.6%)
	To Eat = To Place:	51.1 (59.4%)	To Eat = To Place: [35.8%]	35.7 (71.4%)
	Total:	86.0 (100%)	Total:	50.0 (100%)

when the same endings are shown in uniformly distributed forms. Ferro et al. (2010) show that the strategy is advantageous for word processing, since dedicated memory chains minimize the number of one-to-many internode transitions (schematically shown in Fig. 3, right), thus reducing the degree of uncertainty in accessing/recalling a word form.

All in all, experiments 1 and 2 support Fogassi and colleagues' conjecture that the use of goal-specific neural units may enhance execution and recognition of action sequences (especially habitual ones) by reducing uncertainty at the level of their neural coding. Moreover, they are in keeping with a view of working memory as an emergent property of the functional interaction of short-term and long-term memory structures. In TSOMs, long-term temporal expectations make it easier for a map to recall a sequence recoded in a volatile integrated activation pattern, enhancing successful prediction of upcoming symbols, in line with behavioral and neuroimaging results (DeLong, Urbach, & Kutas, 2005; Federmeier, 2007).

In spite of their analogies, experiments 1 and 2 present important differences. In experiment 1, action chains are assumed to be activated while *performing* a certain motor behavior, whereas lexical chains in experiment 2 develop upon *perceiving* a certain sequence of letters *out of context*. Accordingly, while an action intention is set before the beginning of a chain of movements and already affects the first motor act, we could not simulate a similar effect with lexical chains for *context-free* word recognition. More ecological assumptions concerning the way words are administered to a lexical map and a more articulated lexical architecture including levels of lexico-semantic representation will allow us to simulate such a goal-oriented predictive bias. Finally, although motor and lexical chains are assumed to insist on different cortical areas (IPL and STG, respectively), the role of IPL as a critical interface between auditory and motor-based representations is consistent with the idea that IPL can support, in addition to frontal regions, the development of sensory-motor chains for lexical repetition/rehearsal.

8. Concluding remarks

Common computational principles of memory self-organization and predictive learning may underlie storage and processing of lexical and action chains in the primate brain. The hypothesis is compatible with what we know about the neuroanatomical network supporting working memory and sequential cognition. Our computational architecture shows that common principles could guide the development of memory structures supporting efficient processing in both action and linguistic domains. Neuroanatomical studies of monkeys' sensorimotor networks reveal somatotopic organization and chain-like specialization. We do not have comparable evidence of selective activation of dedicated node chains for lexical access/processing. Nonetheless, the parallelism between time-bound learning, working memory, and sequential processing in both goal-directed motor planning and lexical processing lends support to the hypothesis that memory structures and processes in the two domains could be based on identical domain-independent

principles. The actual level of integration between neuroanatomical networks supporting action and linguistic processes remains an open empirical question (Barca & Pezzulo, 2012; Glenberg & Gallese, 2011).

Acknowledgments

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