Broca's area: a supramodal hierarchical processor?

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Abstract

Despite the presence of shared characteristics across the different domains modulating Broca's area activity (e.g. structural analogies, as between language and music, or representational homologies, as between action execution and action observation), the question of what exactly the common denominator of such diverse brain functions is, with respect to the function of Broca's area, remains largely a debated issue. Here, we suggest that an important computational role of Broca's area may be to process hierarchical structures in a wide range of functional domains.

A rapidly growing scientific literature has demonstrated that Broca's area is activated by a multitude of disparate linguistic, cognitive and sensorimotor tasks. Two main factors appear to determine the multi-domain involvement of Broca's area in human brain functions. Firstly, the existence of fine-grained cytoarchitectonic parcellations within both Brodmann Areas 44 and 45 points to a heterogeneous distribution of functions in Broca's area (Amunts et al., 1999). Depending on the task investigated, distinct sub-regions of Broca's area are found to be activated. For instance, *pars opercularis* and *pars triangularis* appear to process different language components (Bookheimer, 2002). Secondly, depending on the task, Broca's area is activated in conjunction with task-specific combinations of other brain regions – compatible with the view that the neuronal populations of distinct sub-regions of Broca's area are connected in a unique manner with other brain regions. These observations are suggestive of a fine-grained functional parcellation within Broca's area rather than of a unique, supramodal role of Broca's area across different brain functions. However, functional parcellation and supramodal computations are not two mutually exclusive mechanisms and could cohexist. Broca's area may display sub-regional computational specializations, some of which may underlie many different functional domains. Supramodal mechanisms are indeed pervasive within the prefrontal cortex and allow a diverse range of information to be synthesized, processed and stored at an abstract level (Duncan, 2001; Miller, 2000). In this respect, a perspective that has not been explored in great detail is that of isolating the structural properties of tasks involving activity in Broca's area and examining them with respect to a cognitive theory, giving particular attention to the computational demands involved.

The idea on which this position paper is focused, namely that the processing of different hierarchical structures depends on Broca's area, is not altogether new. Hierarchical structures are a distinctive property of natural languages, either spoken or signed (Hauser et al., 2002). Hierarchical structuring is also to be found across several typically human, non-linguistic functional domains such as object manipulation, visuospatial processing, and music (for recent reviews, see: Patel, 2003; Tettamanti, 2003). Non-human primates are not capable of spontaneously extracting hierarchical structural regularities that humans can easily detect (Fitch and Hauser, 2004; Jackendoff, 1999).

Convergent experimental evidence suggest that Broca's area plays an essential role in this human specific faculty (Greenfield, 1991; Friederici, 2004). For example, the acquisition of language and action-related behaviors (such as object manipulation, tool use and gestures), both involving Broca's area, appear to correlate with respect to increasing hierarchical structural complexity and time course of acquisition (Bates and Dick, 2001; Greenfield, 1991). Recent empirical findings have substantiated this hypothesis. Tettamanti and colleagues (2002) showed that, in healthy adult subjects, the acquisition of novel grammatical rules conforming to the universal language format (i.e. having a hierarchical structure), as opposed to novel non-grammatical rules that do not conform to such format and are never found in human languages (i.e. not having a hierarchical structure), selectively activates left perisylvian regions including Broca's area *pars opercularis*. The implications of these results have received support by a study of Musso and colleagues (2003), showing that hierarchy within grammatical structures can modulate activity in

Broca's area across a wide-range of typological grammatical variations, such as found between Japanese and Italian.

Other studies on syntactic processing have varied the level of (hierarchical) syntactic complexity, either aspecifically (see Caplan, 2001 for a review) or specifically (Ben-Shachar et al., 2003; 2004). All these studies have found activations in the left inferior frontal gyrus, within and around Broca's area. Crucially, however, none of them included a comparison between hierarchically organized structures and structures *lacking* a hierarchical organization.

As for action-related behaviors, the need for a hierarchical organization in behavior has been recognized many decades ago (Lashley, 1951; Dawkins, 1976). It has been proposed that complex sequences of actions, such as in tool use, are hierarchically structured (Byrne and Russon, 1998). To our knowledge, hierarchy in the organization of action has not been the object of specific investigation as yet. However, several lines of research suggest that Broca's area plays a role in processing action-related knowledge. For instance, when comparing observation of meaningful (e.g. hammering a nail) with meaningless action pantomimes, Decety and colleagues (1997) found a selective activation of Brodmann's area 45. In a different experiment, it was shown that the observation of videotaped actions performed with the hand and the mouth activates Broca's area (Buccino et al., 2001). Broca's area may also be crucial for action understanding mediated by language, as shown by two recent experiments in which subjects listened to either words (Hauk et al., 2004) or sentences (Tettamanti et al., in press) describing actions performed with different body parts. The latter findings suggest that Broca's area may process action knowledge at a higher cognitive level of abstraction.

However, such observations do not warrant the conclusion that Broca's area is a supramodal hierarchical processor. Hierarchical structures can differ considerably with respect to typology and complexity. In developing an anatomo-functional model of Broca's area as a supramodal hierarchical processor, the variation of hierarchical structures within and across different functional domains needs to be given due consideration.

Along what lines may a domain-independent approach to hierarchical processing be developed? In setting up a typology of hierarchical relations underlying the processing of such diverse entities as linguistic clauses and sequences of non-linguistic symbols (e.g. musical tones or gestures) structural variables – such as the number of hierarchical levels underlying a specific structure and the number of conformations that a particular structure can take – must be taken into account. The assumption is made that there are (psychological) boundaries linking elements within a stuctured sequence, as for instance the words in a sentence[1]. Accordingly, boundaries linking some element to a particular higher-order level can be arranged in a given number of conformations (e.g. words in a phrase may have to be in a fixed order to achieve communicative intents). The process of selecting one or more well-defined conformations is here taken to be tied up to a computational cost; the greater the number of conformations that need to be discarded from the set of all possible conformations, the higher the computational cost (either in composing or decomposing the structures). In other words, the computational cost associated with a particular hierarchical stucture depends on the

[1] The fact that there are boundaries between linguistic elements is a well-established psycholinguistic fact (Levelt, 1989).

conformational degrees of freedom displayed by the elements constituting the structure. A few examples may help in clarifying this point.

Let us take a set of three identical symbols (X, X, X) arranged in a non-hierarchical structure S_n(X,X,X) (Figure 1A). The structure S_n(X,X,X) is mirror-symmetrical: the structural conformations generated by exchanging structural boundaries across the central, vertical symmetry axis are non-distinguishable. There is only one structural conformation that maps the three elements (X,X,X) onto the higher-order string 'XXX'. The number of distinguishable conformations (C) is C=1. By definition, if C=1, then Γ =0, where Γ is the computational cost[2].

Now consider the hierarchical structure S_h(X,X,X) and its mirror symmetric S_h(X,X,X)' (Figure 1B). There are two distinguishable, mirror-symmetric, structural conformations that map the three elements (X,X,X) onto the string 'XXX'; therefore C=2. The choice of one particular conformation (i.e. discarding one of the two possible conformations) is associated, by definition, with a computational cost Γ =1. In general, Γ =C_d ,where C_d is the number of discarded conformations from the set of all possible conformations.

Let us introduce a different case, where a set of three distinct elements (X, Y, Z) is arranged in a hierarchical ordered structure S_h(X,Y,Z) and its mirror symmetric structure S_h(X,Y,Z)' (Figure 1C). The number of possible conformations is given by the permutation (P) of the three elements, multiplied by two, to account for the fact that each conformation is associated with its mirror-symmetric; i.e. C = 2[P(3)] = 12. The choice of one and only one particular conformation (i.e. discarding 11 conformations) is associated with a

[2] We do not imply that no computational cost is associated with this process. But as the complexity of S_n(X,X,X) is minimal, we arbitrarily take it here as the null baseline.

computational cost Γ =11.

As may be inferred from these few examples, a hierarchical organization allows one to establish univoque relations that would not be captured by non-hierarchical structures. On the other hand, univocity and complexity are associated with a computational cost, which – given a fixed number of elements – is higher for hierarchical than for non-hierarchical structures.

What is the practical impact of these briefly sketched theoretical considerations? Let us consider a few examples, either of a linguistic or a non-linguistic nature, and see if we can estimate the computational cost associated with each structure. Let us take a string of three English words (the, dog, barks) mapped onto the hierarchical structure[3] S_h(the, dog, barks) (Figure 1D). Many of the theoretically possible conformations (C = 2[P(3)] = 12) do not conform to the positional syntactic rules of English (e.g. [barks (dog the)] or [(the barks) dog]). Indeed, there is only one possible conformation in English, therefore C_d=11, and Γ =11.

The point being made can also be demonstrated by a non-linguistic case concerning tool use. Children between 11 and 20 months were observed during self-feeding with a spoon (Connolly and Dagleish, 1989; Greenfield PM, 1991). Depending on developmental age, the children combined spoon (s), food (f) and mouth (m) in different ways; with increasing age some of the combinations followed a hierarchically ordered structure S_h(s,f,m). By learning the (hierarchical) relations governing spoon use, the child ends up excluding a number of combinations from the set of all possible ones (C = 2[P(3)] = 12), such as for instance [(s m) f] – i.e. taking the spoon to the mouth and then

[3] Here and in the following, we leave aside linguistic notations (see e.g. Haegemann, 1994). This simplification helps to illustrate the principles more clearly. The principles discussed here can be extended to meet more refined analyses.

touching food with both. Eventually, children of 19-20 months end up converging on the viable hierarchical relations [(s f) m] – i.e. bringing the spoon with food to the mouth – and [m (s f)] – i.e. moving the mouth to the spoon-food combination (Figure 1E). The associated computational cost is $C_d = \Gamma = 10$.

These crude examples are only meant to illustrate the general principle: both language syntax and tool use are hierarchically organized. As discussed in the introduction, both hierarchical syntactic and action-related knowledge appear to elicit activations in Broca's area. Is hierarchical organization an explanatory factor for the shared neural representations? Particular caution is required in responding to this question. Whenever the processing of perceptually discrete elements calls for structural integration, some kind of syntactic processing is taking place. As pointed out by Patel (2003) it is a matter of developing cognitive theories of processing that capture the hierarchical principles inherent in the particular functional domains. The approach sketched here is simplified but it takes into account the fact that information processing relies on keeping track of structural dependencies and performing structural integration. Gibson's theory of sentence processing (1998) also rests on the notion of integration and memory resources, however, the emphasis here is on the typology of hierarchical structures and the constraints by which they are governed. If these constraints are not carefully considered, a reasonable comparison of the neural structures subserving different functional domains is not possible. A theory-driven computational analysis can help in understanding the evolutionary and developmental contribution of Broca's area with respect to hierarchically organized linguistic and non-linguistic functions.

References

AMUNTS K, SCHLEICHER A, BUERGEL U, MOHLBERG H, UYLINGS HBM, and ZILLES K. Broca's Region Revisited: Cytoarchitecture and Intersubject Variability. *Journal of Comparative Neurology,* 412: 319-341, 1999.

BATES E and DICK F. Language, gesture, and the developing brain. *Developmental Psychology,* 40(3): 293-310, 2002.

BEN-SHACHAR M, HENDLER T, KAHN I, BEN-BASHAT D, and GRODZINSKY Y. The neural reality of syntactic transformations: Evidence from functional magnetic resonance imaging. *Psychological Science,* 14: 433-440, 2003.

BEN-SHACHAR M, PALTI D, and GRODZINSKY Y. Neural correlates of syntactic movement: Converging evidence from two fmri experiments. *Neuroimage,* 21: 1320-1336, 2004.

BOOKHEIMER S. Functional MRI of language: new approaches to understanding the cortical organization of semantic processing. *Annual Review of Neuroscience*, 25: 151-188, 2002.

BUCCINO G, BINKOFSKI F, FINK GR, FADIGA L, FOGASSI L, GALLESE V, SEITZ RJ, ZILLES K, RIZZOLATTI G, and FREUND H-J. Action observation activates premotor and parietal areas in a somatotopic manner: An fmri study. *European Journal of Neuroscience,* 13: 400-404, 2001.

BYRNE RW and RUSSON AE. Learning by imitation: A hierarchical approach. *Behavioral and Brain Sciences,* 21: 667-721, 1998.

CAPLAN D. Functional neuroimaging studies of syntactic processing. *Journal of Psycholinguistic Research,* 30: 297-320, 2001.

CONNOLLY KJ and DALGLEISH M. The emergence of tool-using skill in infancy. *Developmental Psychology,* 25(5): 894-912, 1989.

DAWKINS R. Hierarchical organization: A candidate principle for ethology. In Bateson P.P.G. and Hinde R.A. (Eds.) G*rowing points in ethology.* Cambridge, Cambridge University Press, 1976, pp. 7-54.

DECETY J, GRÈZES J, COSTES N, PERANI D, JEANNEROD M, PROCYK E, GRASSI F, and FAZIO F. Brain activity during observation of actions. Influence of action content and subject's strategy. *Brain,* 120 (10): 1763-1777, 1997.

DUNCAN J. An adaptive coding model of neural function in prefrontal cortex. *Nature Reviews Neuroscience*, 2(11): 820-829, 2001.

FITCH WT and HAUSER MD. Computational constraints on syntactic processing in a nonhuman primate. *Science*, 303(5656): 377-380, 2004.

FRIEDERICI AD. Processing local transitions versus long-distance syntactic hierarchies. *Trends in Cognitive Sciences*, 8(6): 245-247, 2004.

GIBSON E. Linguistic complexity: locality of syntactic dependencies. *Cognition*, 68: 1-76, 1998.

GREENFIELD PM. Language, tools and brain: The ontogeny and phylogeny of hierarchically organized sequential behavior. *Behavioral Brain Sciences*, 14: 531-595, 1991.

HAEGEMANN L. *Introduction to Government and Binding Theory*. Oxford: Blackwell, 1994.

HAUK O, JOHNSRUDE I, and PULVERMULLER F. Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, 41(2): 301-307, 2004.

HAUSER MD, CHOMSKY N, and FITCH WT. The faculty of language: what is it, who has it, and how did it evolve? *Science*, 298: 1569-1579, 2002.

JACKENDOFF R. Possible stages in the evolution of language. *Trends in*

Cognitive Sciences, 3(7): 272-279, 1999.

LASHLEY KS. The problem of serial order in behavior. In Jeffress L.A. (Ed.) *Cerebral mechanisms in behavior: The hixon symposium*. New York: Wiley, 1951, pp. 112-146.

LEVELT WJM. *Speaking: from intention to articulation*. Cambridge, MA: MIT Press, 1989.

MILLER EK. The prefrontal cortex and cognitive control. *Nature Reviews Neuroscience*, 1: 59-65, 2000.

MUSSO M, MORO A, GLAUCHE V, RIJNTJES M, REICHENBACH J, BUCHEL C, and WEILLER C. Broca's area and the language instinct. *Nature Neuroscience*, 6(7): 774-781, 2003.

PATEL AD. Language, music, syntax and the brain. *Nature Neuroscience*, 6(7): 674-681, 2003.

TETTAMANTI M, ALKADHI H, MORO A, PERANI D, KOLLIAS S, and WENIGER D. Neural correlates for the acquisition of natural language syntax. *Neuroimage*, 17: 700-709, 2002.

TETTAMANTI M. *Language acquisition and processing: hierarchically organized cognitive processes*. Ph.D. Thesis, Zurich: Univesity of Zurich, 2003.

TETTAMANTI M, BUCCINO G, SACCUMAN MC, GALLESE V, DANNA M, SCIFO P, FAZIO F, RIZZOLATTI G, CAPPA SF, and PERANI D. Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of Cognitive Neuroscience*, in press.

Figure 1: Hierarchical and non-hierarchical structural conformations