The dynamics of language-related brain images

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The advent of functional brain imaging has renewed our knowledge of the brain correlates of cognitive processes. Based on different physical principles, Positron Emission Tomography (PET), functional Magnetic Resonance Imaging (fMRI), and multi-channel Electro- or Magneto-Encephalography (EEG, MEG) make it possible to measure *changes* in various indices of ongoing neural activities arising from the brain 'in action.' These techniques soon became popular because they produce suggestive colorful 'maps', intuitively perceived as the neural anatomy of cognitive functions such as language processing. Despite the revolutionary input of neuroimaging, conceptualizations of the language/brain relationships are still too static. 'Neuroimages' do not just consist of maps of the crucial nodes activated within large-scale neural systems throughout the brain. They should rather be viewed as representations of *transient* states and time series of activities in these systems. However, the time scale which defines such transient states varies largely from the ms order for EEG and MEG to a few seconds for fMRI and a few minutes for PET. Language, as a high-speed process of incoming information and real-time programming of responses, is a typical example in which it is critical to consider the dynamics of the ever-changing functional status of its neural counterparts (for a review, Démonet *et al.*, in press).

Here we focus on some examples of recent fMRI studies in which the dynamics of neural responses have been considered, for different levels of language representations and types of experimental settings. These works were presented in a session devoted to language at the first meeting of European neuropsychological societies. Considered from both the methodological and neuro-linguistic points of view, these studies may guide future experiments to understand better the spatial temporal dynamics of the physiology of language. The first study relates to physical discrimination and categorisation of letters and distractors (Pernet *et al.*, in press), the second example addresses priming effects in lexical decision tasks (Kouider *et al.*), and the third is devoted to *learning* new grammatical rules (Musso *et al.*, 2003). At different time scales, these studies all addressed the adaptive properties of language-related neural systems depending on task requirements, especially by reference to either automatic or controlled memory processes.

## Differential time course of neural activities subserving letter processing

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The interaction between categories of stimulus (Latin letters, geometrical figures and Korean letters) and two different processes (within-category visual discrimination versus categorization, i.e., across-category classification of items) was analyzed for both the spatial distribution of the activated areas and the temporal dynamics of the corresponding BOLD signals (Thierry *et al.*, 1999 and 2003). Subjects performed a same/different task, responding for items that differ and not responding for identical stimuli. For the discrimination task, subjects detected local unmatched features between categorically identical items (e.g., T T) whereas for the categorization task, subjects detected pairs in which each item pertained to different categories (e.g., L ⌂, latin letter and geometrical figure respectively).

From the spatial extent analysis, a common cerebral network, that encompassed the striate and extrastriate areas (especially the fusiform gyri), the precunei, the insulae, the dorsal frontal cortex (DFC) and the cingulate gyrus, was observed across conditions. Within this network, amplitude values and spatial maxima variations were observed with a stronger involvement of the left DFC for known stimuli (letters and geometrical figures) in comparison with the right DFC that was more involved in the visuo-spatial processing. Using a Region of interest (ROI) analysis procedure, we observed separate effects on BOLD amplitude and latency according to stimulus and/or process. Noticeably, the time course of the signal differed across ROIs and tasks. The discrimination task exhibited a posterior-to-anterior pattern in both hemispheres with earlier responses starting from the fusiform gyri, going next to the precunei, then to the DFC bilaterally and finally to the insulae. For the categorization task fastest latencies were also observed in the fusiform gyri but then, activations were fastest in the right hemisphere (precuneus and DFC), next in the left DFC and precuneus, and finally the longest latencies were again observed in the insulae (Figure 1).

These results demonstrated the involvement of a common cerebral network for both tasks with major influence of stimulus
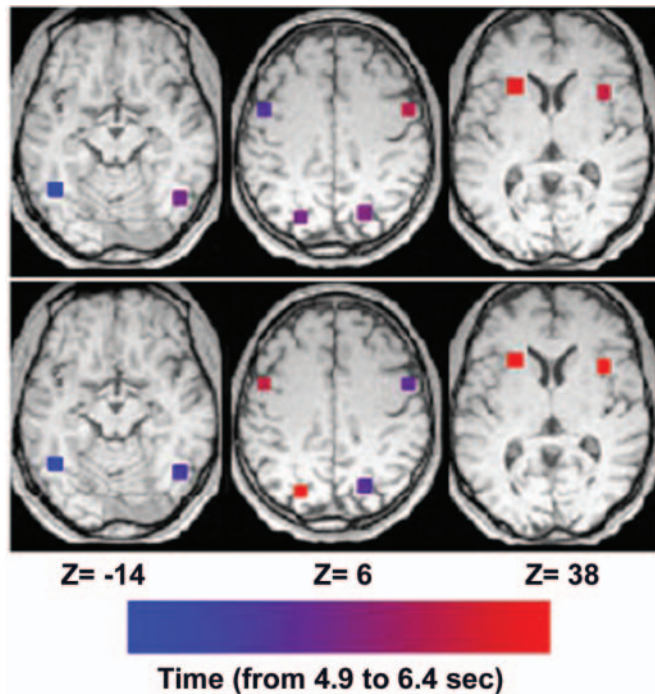
Fig. 1. Color coding in the table corresponds to *latencies* of the peak of the hemodynamic response studied with fMRI, from early (blue) to late (red) latencies, observed in the inferior temporal cortex, precuneus, dorsolateral frontal cortex and insula, in a group of 12 subjects performing either a categorisation task (bottom row) or a within-category discrimination task (top row) for letters and other graphic stimuli (from Pernet et al., in press).

types on amplitudes during the categorization task, reflecting access to letter representation in visual long-term memory. The influence of task features on latencies suggested a parallel versus cooperative processing across hemispheres relating to the discrimination and categorization tasks respectively. The differential engagement of components of a common network over time depending on task requirements emphasizes the role of cortical dynamics during cognitive processes.

Priming effects in lexical decision tasks

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This work focused on the controversial issue of subliminal perception. The authors asked whether the basic codes implied during word reading (i.e., orthographic, phonological, semantic) are involved and interact subliminally, or whether conscious stimulus perception is necessary for these codes to be processed. Using priming paradigm, Kouider *et al.* show that priming effects with subliminal, unconscious processing of the primes occur when prime-target pairs share either the same lexical representation (e.g., clip - CLIP) or
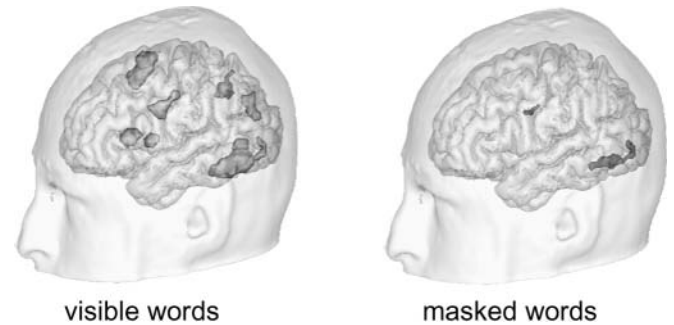
Fig. 2. Group activations in the left hemisphere only, as seen through translucent three-dimensional reconstruction of the skull and brain of one of the participants. In these transparent views, the deep activations in fusiform, parietal and mesial frontal cortex appear through the overlying lateral cortices (from Dehaene et al., 2001).

main orthographical features (e.g., plip - CLIP). This subliminal lexical analysis implies the involvement of *abstract* orthographic representations, as priming occurs regardless of the physical dis/similarity of target and prime. By contrast, priming resulting from the interaction of orthographic and phonological codes (e.g., advantage for homophonic pairs such as klip-CLIP), as well as cross-modal (visual-auditory) repetition priming or semantic priming, was shown to be correlated with prime awareness. As an illustration of the neural counterparts of the subliminal *versus* conscious priming effects, results from a recent study by Dehaene *et al.* (2001) were presented (see Figure 2). In this study, the activation to subliminal words remains restricted to a subpart of the left fusiform gyrus labelled as the "Visual Word Form Area" and responsible for computing an invariant structural representation of words as ordered sequences of abstract letter formats, invariant for size, font, and case. By contrast, conscious perception was associated with activities in a large network which, in addition to the VWFA, included inferior prefrontal/insular, parietal, and anterior cingulate areas, probably reflecting additional computations occurring in conscious priming conditions. Depending on specific experimental features (e.g., exposure duration of stimuli, presence of a mask) the dynamics of the neural systems involved in reading may be either restricted to relatively early stages of processing or spread to the entire network.

Learning natural and arbitrary grammatical rules in foreign languages: the crucial role of Broca's area
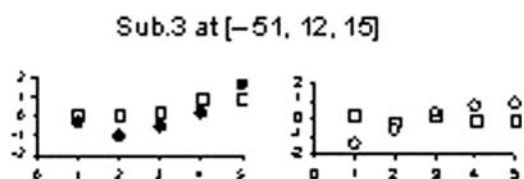
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Several lines of evidence suggest that the left inferior frontal lobe is predetermined for language. fMRI was used to investigate
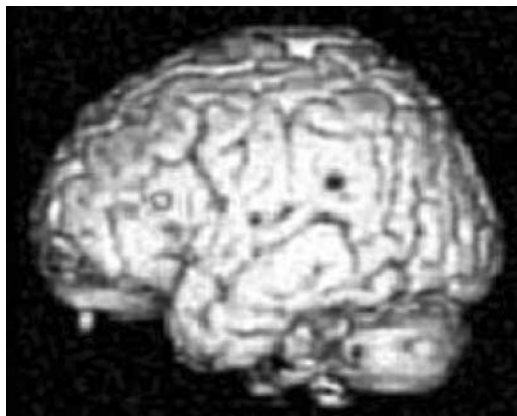
Fig. 3a. Result of the interaction between performance and type of rule learning (real versus arbitrary Italian in red, real versus arbitrary Japanese in yellow).

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Fig. 3b. Rule learning in 5 sessions observed in one subject from Musso et al's experiment (2003). Scatterdram showing changes over time in BOLD signal in the left inferior premotor cortex (Broca's area) (open squares) and in performance on learning of real rule (filled squares) and arbitrary rule (open circles).

whether Broca's area is epigenetically determined for the acquisition of a new language. The experiment was performed in 16 German native speakers, who were naïve towards Italian and other Roman or Oriental languages while learning during fMRI sessions (1) three real grammatical rules of Italian or Japanese and (2) three arbitrary rules using Italian or Japanese vocabulary. The real rules used from Italian or Japanese can be considered examples of "natural" rules of language, because they follow universal principles of grammar as defined by Chomsky. In the arbitrary grammatical rules which were designed, the relationships between nominal and verbal elements are disregarded to determine the sentence organization. These arbitrary rules merely rely on the linear order of words in the sentence, instead of considering the hierarchical structure of noun and verb clauses, e.g.,

the typical structure subject-verb-object that is prevalent in several western languages. Subjects, who were unaware of the nature of the different rules, learned the natural and unnatural rules similarly without significant difference in performance. A random effect analysis showed that whereas rule learning, whatever its nature, correlates with increase of activity in the right DFC, a significant interaction effect between learning performance and type of rule learning ("natural" > "arbitrary") is observed only in the *left* inferior frontal gyrus (i.e., Broca's area). Activation in Broca's area was specific for "real language" acquisition, indicating a unique neural response pattern so that biological constraints and language experience interact to enable building up linguistic competence in a new real language.

Overall these three studies appear as interesting examples in which functional neuroimaging was used to explore various dimensions of the dynamics of the complex neural systems coming into play in these various experimental contexts. This approach appears extremely fruitful for future studies devoted to still poorly understood, although crucial, dimensions of the neural implementation of language functions, such as the respective correlates of automatized (implicit) and controlled (explicit) processes (Ullman, 2004).

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