

DISTINCT AREAS IN PARIETAL CORTEX INVOLVED IN LONG-TERM AND SHORT-TERM ACTION PLANNING: A PET INVESTIGATION

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ABSTRACT

The sequential organization of events within a script, can be considered as a means to explore the cognitive mechanisms involved in action planning. Scripts are composed of goal-oriented sequences of events that typically occur in a specific and systematic order. The purpose of this study was to investigate the effect of temporal variation between script events (*short-term* versus *long-term*) on neural activity in normal volunteers. Subjects were required to judge whether the chronological order of three events was correct or not, while regional cerebral blood flow was measured using positron emission tomography. The modality of script presentation (graphic versus lexical) was manipulated.

In the left hemisphere, the supramarginal gyrus, the middle frontal gyrus, the inferior temporal gyrus, and the middle occipital gyrus were more activated in the short-term script conditions, while the angular gyrus, the medial superior frontal gyrus, the precuneus bilaterally, the anterior cingulate gyrus and the inferior and middle temporal gyrus on the left were more involved during long-term scripts processing. The occipito-temporal junction (MT/V5) was significantly more activated in the graphic conditions as compared to the lexical ones, and in the short-term scripts conditions as compared to the long-term ones although all stimuli were static. Our results support the notion that two distinct frontal-parietal networks are engaged in short-term and long-term script processing. In addition, our study demonstrates two kinds of dissociations in the parietal lobe. A macro-dissociation between the anterior and the posterior portion of the inferior parietal lobe was found which accounts for processing short-term and long-term scripts respectively, as well as a micro-dissociation in each of these regions which is associated with distinct processing depending on the presentation modalities. These results may help to better understand apraxia at the neurophysiological level.

Key words: intention, action sequence, chronological order, action duration, human, neuroimaging, parietal cortex, IPS

INTRODUCTION

It is generally acknowledged that an action involves several information processing stages, such as intending, planning, programming and executing (Jeannerod, 1995). The first three processes define the aim, the strategy and the appropriate motor plan to achieve the goal, while the last one, the execution phase, is the only one which can be directly observed because it objectively modifies the environment. Neuroimaging techniques provide an in vivo access to the neural correlates of cognitive activity that takes place before the execution of an action. In this study we aimed to explore the neural substrate associated with

the planning stage using positron emission tomography (PET). The use of scripts event-ordering is a means to address the cognitive activity occurring during action planning at a covert level. A script is composed of goal-oriented sequences of events that typically occur in a specific and systematic order (Schanck and Abelson, 1977). The sequential order is certainly one of the main aspects of a script and probably the feature that weighs most on planning activity (Grafman, 1995).

Neuropsychological investigations have compared the performances in script-events ordering in normal subjects and in patients with lesions in the prefrontal cortex and in the posterior temporo-parietal cortical regions. Using a word fluency task, Sirigu et al. (1995b) asked subjects to perform a script generation task in which they had to evoke actions necessary to accomplish a stated goal. Patients with focal damage involving the dorsolateral or the medial prefrontal areas were selectively impaired in what the authors called the action "syntax", that is the capacity to place script elements in their correct order of execution, to stay within the fixed boundaries of the plan, and to make judgements about the importance of actions with regard to the stated goal. Interestingly, while patients with prefrontal lesions were unable to formulate and evaluate a plan of action, they were however capable of retrieving the single actions related to a script activity. These results led the authors to propose that two distinct cognitive modes of representing actions are likely to exist. The first, the syntax mode, is necessary for encoding and retrieving the structural features of action knowledge, such as the conditional relations and the temporal sequence between the action components. This type of processing would require the intervention of the prefrontal areas. The second, mainly refers to the semantic aspect of action processing such as access to the knowledge data base required to assemble a plan. This second mode is hypothesized to engage the posterior associative areas at the temporo-parietal junction (Sirigu et al., 1995b, 1996).

Furthermore, it has been reported that so-called agrammatic patients, with lesions in Broca's area, ordered groups of words correctly to form a logical sequence of actions while they were severely impaired when similar words had to be ordered as a syntactically well-formed sentence. Patients with dorsolateral (common lesion Brodmann's area, BA 46) prefrontal lesions presented the opposite performance, namely a preserved ability to order words to construct a sentence while showing an impairment in sequencing words when these referred to a plan of action. These results suggest that sequence processing may be specific to knowledge domains and may depend on different neural networks within the frontal lobes (Sirigu et al., 1998).

Script processing has also been investigated in healthy subjects by means of neuroimaging techniques. For instance, Partiot et al. (1996) using positron emission tomography showed that scripts categorization and scripts order verification are processed by distinct brain networks within the prefrontal and the temporal regions. Recently a Functional Magnetic Resonance imaging (fMRI) study, conducted by Crozier et al. (1999) using scripts and sentences as stimuli, demonstrated that action sequence and word sequence processing are associated with activation of partially overlapping regions in the left frontal, parietal and temporal cortices. These fMRI results are in agreement with the

patient data described above (Sirigu et al., 1998), and suggest that sequence processing at the sentence and script level may be subserved by specific representations within the prefrontal and parietal cortex. One main objection that can be put forward about these studies however is that ordering words at the syntactic level involves the use of a grammatical rule while ordering words referring to actions is mainly accomplished using a temporal dimension. Given that the chronological order of an action is a crucial aspect in planning, one could ask whether variation in duration (time interval on which the chronological rule has to be applied) of the action sequence could modulate the brain regions recruited during scripts planning. For instance, an activity such as “hammering” requires a series of events that are executed in a narrow time window while an activity such as “renting an apartment” involves events spaced on a longer time scale. There are clues from neuropsychological observations which lead to the hypothesis that short-term actions and long-term actions may not be subserved by the same neural substrate. For example Lehmkuhl and Poeck (1981) have shown that patients with ideational apraxia (IA) failed in a test requiring a sequential structuring of common everyday actions (script event ordering e.g. making a phone call). The same patients however showed unimpaired performance similarly to patients without IA, in a task requiring the serial ordering of pictures which depict events that do not involve object manipulation. In general, apraxic patients with lesions in the inferior parietal cortex usually show severe disturbances in the execution and even in the representation of gestures or what we call here short-term actions while they remain able to engage in long-term planning (De Renzi, 1989; Sirigu et al., 1995a). In contrast, as described above, patients with prefrontal lesions seem to be more impaired in long-term action planning as compared to short-term sequence execution (Sirigu et al., 1995b, 1996; 1998). In this study, we focused on the chronological aspect of action sequence, and investigated whether temporal contiguity between actions could modulate the neural network engaged during scripts processing. Brain regions expected to be involved are mostly the parietal and the frontal lobes given their contribution in action planning. Furthermore, taking into account that patients with “modality specific apraxia” have distinct impairments in gesture execution when action is verbally or visually triggered (Heilman, 1973; De Renzi et al., 1982), we introduced in our paradigm the parameter of modality presentation, which could be either lexical (written sentences) or graphic (drawings). We hypothesized that short-term actions may be planned and represented in a more sensorimotor way as compared to long-term actions and that a distinction in the parietal cortex in particular could be highlighted between the two presentation modalities.

MATERIALS AND METHODS

Subjects

Ten healthy right-handed male volunteers (age 19 to 25 years) with no history of neurologic or psychiatric illness were studied. All subjects gave written informed consent according to the Helsinki declaration. The study was approved by the local Ethic Committee, and subjects were paid for their participation.

Activation Paradigm

Subjects were scanned during four target conditions: short-term scripts with lexical presentation (STL), short-term scripts with graphic presentation (STG), long-term scripts with lexical presentation (LTL), long-term scripts with graphic presentation (LTG). Each condition was replicated twice (8 scanning conditions per subject) and presented in a pseudorandomized order and counterbalanced across subjects.

In all conditions subjects were presented with scripts depicting familiar actions. In each activation condition, twelve scripts pertaining to the same category (i.e. STL, STG, LTL or LTG, see appendix) succeeded one another. A script split an action in three successive events, which were illustrated either by means of drawings in the graphic conditions (LTG and STG, Figure 1-a, b) or by means of sentences in the lexical conditions (LTL and STL, Figure 1-c, d). The three events (drawings or sentences) constituting a script were presented in three neighboring boxes, one for each event describing a step of the action. These three events were displayed at the same time and lasted for six seconds on the screen regardless of the subject's response. Fifty percent of the scripts showed the events in a logical order and fifty percent in a wrong order. Correct and wrong order scripts were randomized in each condition. Subjects were instructed to judge whether the three events of the scripts were in a right or in a wrong order by pressing the corresponding button of the key-pad with their right fingers. To determine whether the sequence of events was correct or not, subjects had to mentally order the three events according to a logical and goal-directed plan. This procedure is considered to covertly trigger action planning process (Schanck and Abelson, 1977).

Short-term Scripts

Stimuli were composed of three events that were temporally close, and which usually occur in the same location (see Figure 1-b, d). Thus, in both STG and STL conditions subjects were presented with very pragmatic, short and daily life actions such as brushing one's teeth, cooking an egg, or smoking a cigarette (cf. Appendix).

Long-term Scripts

Stimuli were composed of three events that were temporally far from one another, and which occurred in different locations (Figure 1-a, c). In LTL and LTG conditions, actions presented in the scripts were more complex and long to be realized but still belonged to the daily life repertoire, like planning a trip, learning lessons to pass an exam or looking for a job (cf. Appendix).

In order to clearly specify the two categories of actions used in the scripts (i.e. short-term and long-term), 10 naive subjects (independent of the experimental subjects who participated in the PET study) were asked to classify 100 scripts depicting common actions upon the criteria of time and location proximity between the three events. Subject evaluated whether the events within every script were close or far, separately for location and time criteria. Then a score out of ten for the two criteria was calculated for each script. Only those scripts that reached a score =17 (out of 20) for the two criteria (time and location proximity for short term scripts and time and location distance for long term scripts) were selected for the PET study. Series of three events considered close, both in time and in location by the subjects according to this procedure, were selected as depicting a short-term action. Similarly, series of three events considered far in time and in locations were selected for depicting a long-term action.

Experimental subjects underwent a short training before each PET-condition. Stimuli used in the training session were different to those used during the scanning session.

Scanning Procedure

PET scans were obtained with a Siemens CTI HR + tomograph (63 slices, 15.5 cm axial field of view) with collimating septa retracted, operating in high-sensitivity mode.

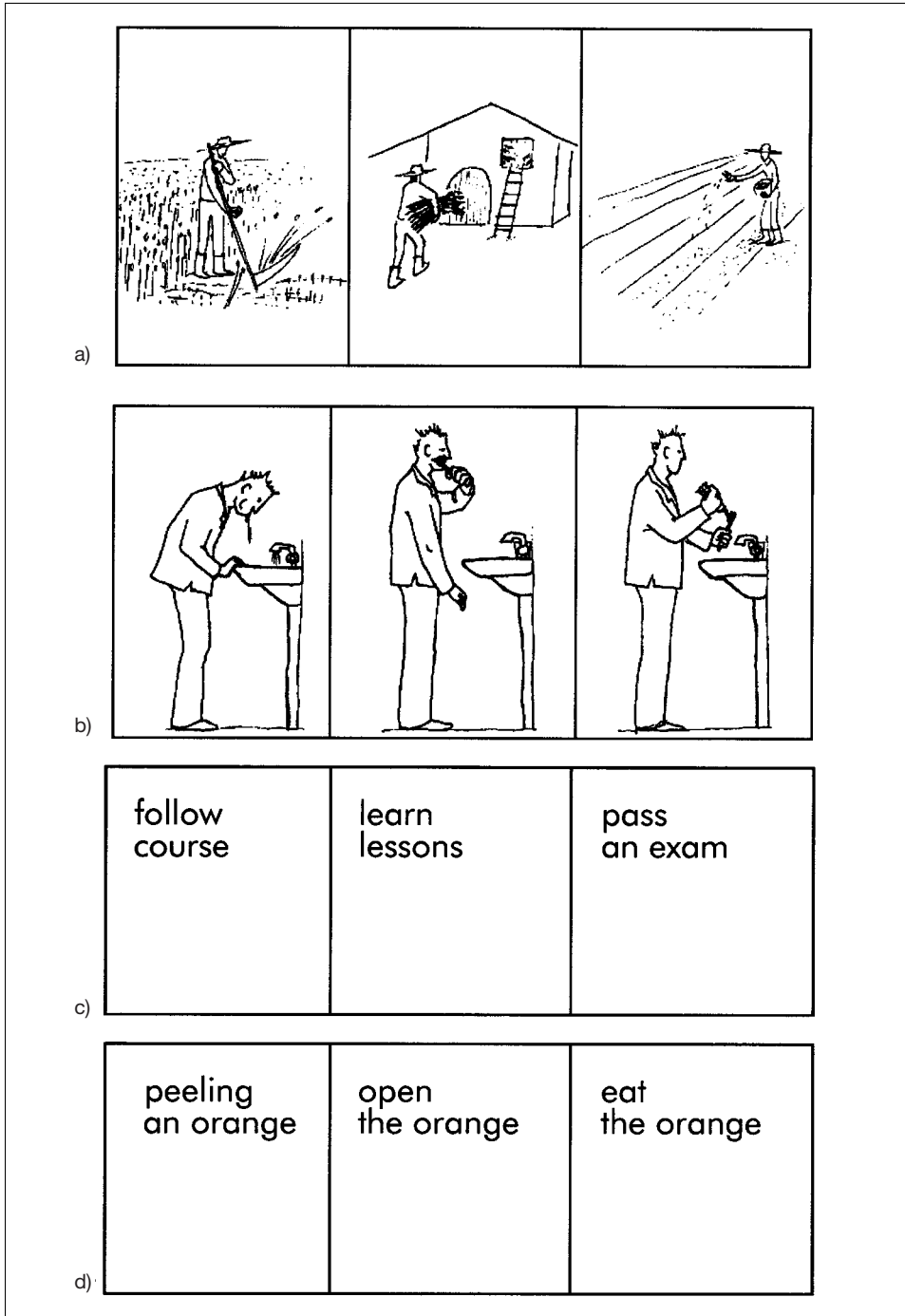


Fig. 1 – Script examples in each category. a) graphic script illustrating a long-term action (LTG); b) graphic script illustrating a short-term action (STG); c) verbal script depicting a long-term action (LTL); d) verbal script depicting a short-term action (STL).

Subjects were installed in supine position on the bed of the camera, and their head was immobilized within a closely fitted, thermally modeled plastic mask. Throughout the PET session, control of head position was made by laser alignment along with reference points on Reid's line before and after each session. A measure of the attenuation parameters was performed using retractable ring sources, just after the subject was properly installed. Changes in rCBF were measured using the intravenous radioactively labeled water ($H_2^{15}O$) bolus method by recording the radioactivity following the intravenous bolus injection of 333 Mbq (9mCi) of $15O-H_2O$ through a forearm cannula placed into the brachial vein. The PET data were acquired during a 60 seconds period starting approximately 30 seconds after the injection. The cognitive stimulation started 12 seconds before the PET data acquisition. Its duration lasted for 72 seconds, enough to cover the whole scanning period. Each condition was separated from the next by a ten minute inter-scan period.

Stimulus Presentation

A NEC projector displayed the stimuli (resolution of 800 by 600) on a screen located at the back of the camera. A mirror placed in front of the subjects' eyes allowed to see the projected images by reflection. The resultant distance from the eyes to the screen was 50 centimeters approximately (corresponding field of view: 42° in the horizontal dimension and 32° in the vertical one). A Power Macintosh computer (Apple Inc.) with the SUPERLAB software was used to monitor the stimuli presentation and to record the subjects' answers (response times and errors). Subjects responded, on a three button pad, with their right fingers.

Data Analysis

Images were reconstructed and analyzed with the Statistical Parametric Mapping software (SPM99; Wellcome Department of Cognitive Neurology, UK; Friston et al., 1995) implemented in MATLAB 5 (Math Works, Natick, MA, USA). For each subject, images were realigned to the first scan then normalized into the MNI stereotactic space. Data were convoluted using a Gaussian filter with a full-width half maximum (FWHM) parameter set to 12 millimeters.

Global activity for each scan was corrected by grand mean scaling. The condition (interest) and subject (confound, fixed effect) effects were estimated voxelwise according to the general linear model. Linear contrasts were assessed to identify the significant difference between conditions, and were used to create an SPM $\{t\}$, which was transformed into an SPM $\{Z\}$ map. The SPM $\{Z\}$ maps were thresholded at $p < 0.001$ non-corrected. Anatomical identification was performed using atlas of Talairach and Tournoux (1988) and of Duvernoy (1991). For illustrations, foci of activation are superimposed on the single subject T1 MRI of SPM 99.

Two main effect analyses were performed. The first was designed to determine which regions were specifically activated in the short-term scripts conditions compared to the long-term ones, irrespective to the presentation modality ((STL+STG)-(LTL+LTG)). The second analysis was calculated to reveal the brain areas specifically involved in long-term scripts conditions compared to the short-term ones, irrespective to the presentation modality ((LTL+LTG)-(STL+STG)).

The main effect of presentation modality ((STG+LTG)-(STL+LTL) and the opposite) was calculated but not presented because it wasn't the purpose of this study to focus on sensory modality processing in itself. For information this main effect shows a clear dissociation between occipital and frontal areas for visual and lexical stimuli respectively.

However, the interaction term between the two factors, i.e. the duration of the action (ST an LT) and the modality of presentation (G and V) was calculated to evaluate whether, among the brain areas activated in the main effect of script duration, some focus showed a differential activity in the two modalities. This effect was calculated according to the following contrasts [(STG-LTG)-(STL-LTL)] masked by the main effect ST versus LT and [(LTG-STG)-(LTL-STL)] masked by the main effect LT versus ST].

Post hoc analysis was used to assess task-related regional activity. It represents rCBF adjusted values in each task, in order to demonstrate the differential involvement of a given brain area in the 4 experimental conditions.

RESULTS

Behavioral Analysis

For all subjects, both response times and accuracy for all conditions were analyzed. The percentage of correct answers was above 80 % in all conditions (Table I). A two-way ANOVA for repeated measures was calculated on reaction times and showed no significant differences between conditions [$F(3, 27) = 0.845$].

TABLE I
Subjects' Performances for Each Condition

Condition	Correct answers (%)	Missing answers (%)	Global performance (%)	Mean reaction times (ms)
STG	91.9 (SD 27.4)	2,5	89,6 (SD 30,6)	3800 (SD 856)
STL	95.9 (SD 20)	9,5	86,7 (SD 34,1)	3892 (SD 1003)
LTG	93.9 (SD 24.1)	5	89,2 (SD 31,1)	3910 (SD 950)
LTL	97.8 (SD 14.7)	5,8	92,1 (SD 27,1)	3993 (SD 835)

Note: Values are calculated from responses of 10 subjects on 24 scripts per condition. SD = standard deviation. A two-way ANOVA for repeated measures showed no significant differences between conditions [$F(3, 27) = 0.845$].

Main Effect Analysis

Planning Short-Term Actions versus Long-Term Irrespective of Scripts Modality

Short-term action planning [(STL + STG) – (LTL + LTG)] was associated with only left hemispheric rCBF increases, in the inferior part of the middle frontal gyrus, the inferior temporal gyrus, the middle occipital gyrus (Ba 19), and a strong focus of activation (both of the z-score and the voxel-size) was detected in the inferior parietal lobule, specifically located in the supramarginal gyrus (Ba 40). See Table II, Figure 2.

TABLE II
Main Effect (STL + STG) – (LTL + LTG)

Brain region	Coordinates				
	L/R	x	y	z	Z score
Supramarginal gyrus (Ba 40)	L	-58	-46	38	4.56
Middle frontal gyrus inferior part	L	-48	36	20	4.08
Middle occipital gyrus (Ba 19)	L	-50	-70	-6	3.76
Inferior temporal gyrus	L	-52	-34	-22	3.78

Note: Foci of significant rCBF increases ($p < 0.001$) during processing short-term scripts vs. processing long-term scripts, irrespective of the presentation modality. Ba = putative Brodmann area. L/R = left and right hemisphere.

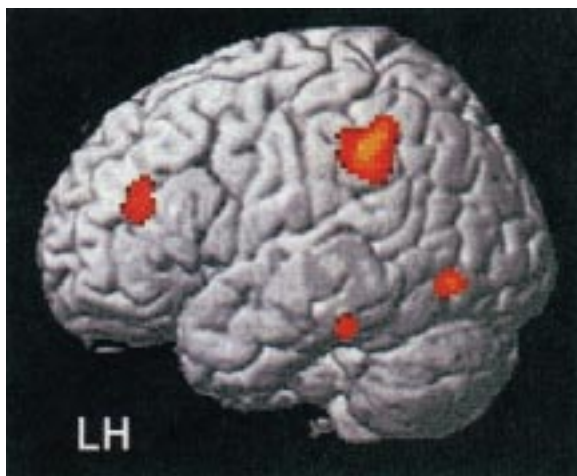


Fig. 2 – Main effect (STL + STG) – (LTL + LTG). Foci of significant rCBF increases ($p < 0.001$) during processing short-term scripts vs. processing long-term scripts, irrespective of the presentation modality. Activation foci are superimposed on the left hemisphere (LH) of the single subject T1 MRI of SPM99.

Planning Long-Term Actions versus Short-Term Irrespective of Scripts Modality

Long-term action planning [(LTL + LTG) – (STL + STG)] was associated with bilateral activation, localized in the angular gyrus (Ba 39), the precuneus and in the medial part of the superior frontal gyrus. In the left hemisphere, activation was detected in the anterior cingulate, and in the inferior and middle temporal gyrus. The fusiform gyrus was activated in the right hemisphere only. see Table III and Figure 3.

TABLE III
Main Effect (LTL + LTG) – (STL + STG)

Brain region	Coordinates				
	L/R	x	y	z	Z score
Angular gyrus (Ba 39)	R	46	-64	24	5.24
Angular gyrus (Ba 39)	L	-48	-64	24	5.21
precuneus	L	-8	-76	38	4.27
Inferior temporal gyrus (Ba 38)	L	-48	0	-40	4.09
Middle temporal gyrus (Ba 21)	L	-62	-16	-12	4.04
Superior frontal gyrus (Ba 9) medial part	L	-14	58	28	3.98
Superior frontal gyrus (Ba 9) medial part	R	4	52	34	3.93
Fusiform gyrus	R	32	-60	-6	3.73
Anterior cingulate gyrus	L	-6	24	-10	3.68
Precuneus	L/R	0	-62	26	3.67

Note: Foci of significant rCBF increases ($p < 0.001$) during processing long-term scripts vs. processing short-term scripts, irrespective of the presentation modality. Ba = putative Brodmann area. L/R = left and right hemisphere.

Interaction Term

Among the brain areas activated in the comparison of short-term versus long-term script [(STL + STG) – (LTL + LTG)] one focus was found to show a differential activity according to the presentation modality. This interaction focus



Fig. 3 – Main effect $(LTL + LTG) - (STL + STG)$. Foci of significant $rCBF$ increases ($p < 0.001$) during processing long-term scripts vs. processing short-term scripts, irrespective of the presentation modality. LH = left hemisphere; RH = right hemisphere.

$[(STG - LTG) - (STL - LTL)] p < 0.001$ masked by the main effect ST versus LT $p = 0.001$ is localized in the ascending segment of the intraparietal sulcus ($x = -52, y = -36, z = 38$; t -value = 4), and shows a difference of activation between short-term and long-term scripts which is significantly greater in the graphic modality as compared to the verbal modality (see Figure 4).

Among the brain areas activated in the comparison of long-term versus short-term script $[(LTL + LTG) - (STL + STG)]$ one focus was found to show a differential activity according to the presentation modality. This interaction focus $[(LTG - STG) - (LTL - STL)] p < 0.001$ masked by the main effect LT versus ST $p = 0.001$ is localized in the ascending posterior segment of the parallel sulcus ($-32, -78, 20$; $z = 3.77$) and shows a difference of activation between long-term and short-term scripts significantly greater in the graphic modality as compared to the verbal modality. The post hoc analysis also shows that this region is involved only in graphic stimuli processing, and within this modality, it exhibits greater activation for long term-scripts (see Figure 5).

DISCUSSION

Although both the stimuli presentation (i.e. scripts) and the task performed by the subjects (i.e. order verification task) were similar across activation conditions and of equal difficulty as demonstrated by the RT analyses (Table I), processing short-term and long-term scripts recruited distinct brain areas in frontal and parietal cortices.

One may notice that, due to our experimental design (no neutral control condition), our study revealed only that part of the neural network which is involved differently in short and long term script.

Short-Term Scripts Planning

Specific activations in relation to short-term planning were found exclusively in left hemisphere, in the middle frontal gyrus, the supramarginal gyrus, the inferior temporal gyrus and in the middle occipital gyrus.

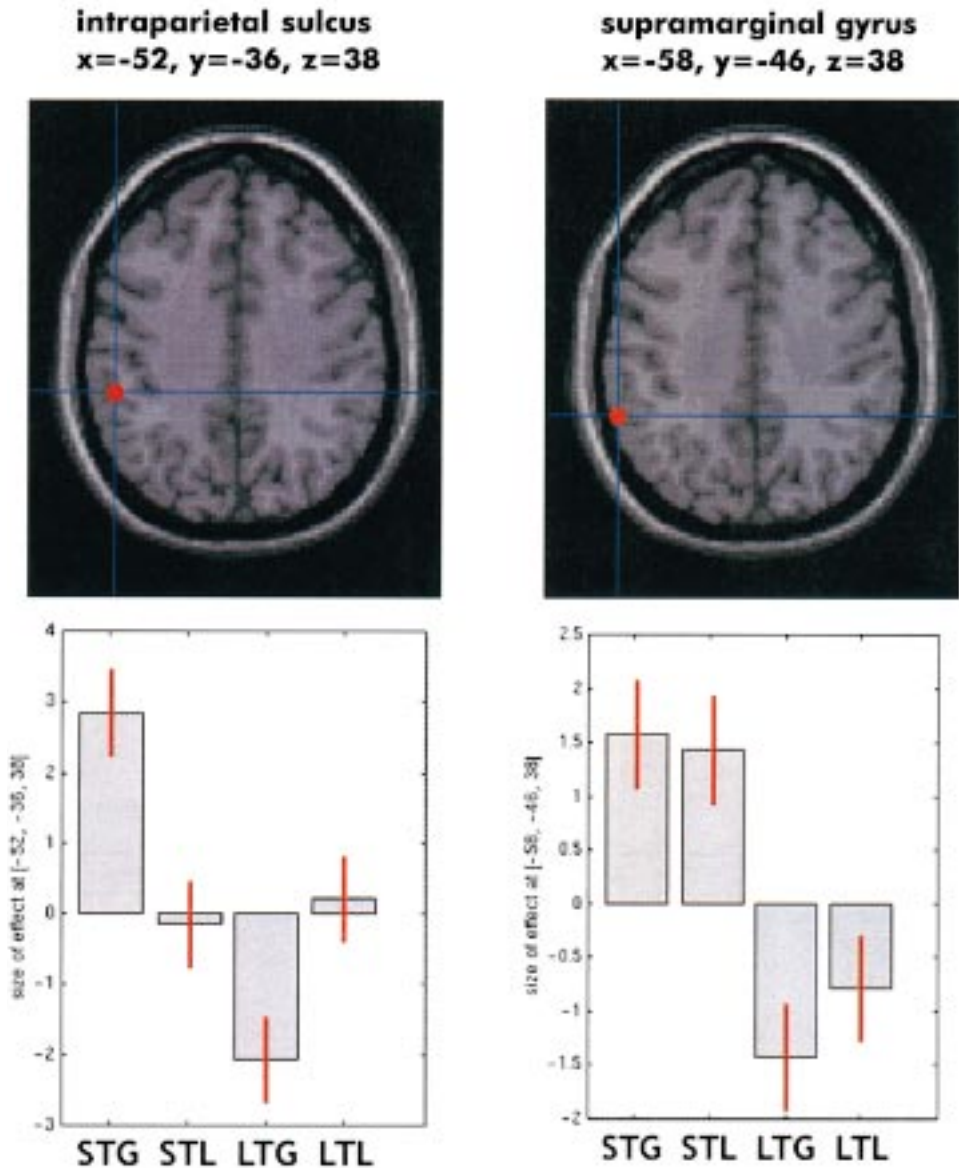
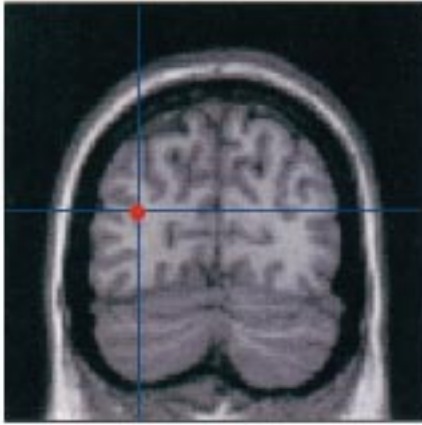


Fig. 4 – *Anatomo-functional dissociation in the inferior anterior parietal cortex for short-term script planning in the two modalities. At the top of the figure, horizontal sections of the brain show precise localisation of peaks of activation in the supramarginal gyrus and in the intraparietal sulcus. At the bottom, results from post hoc analysis are presented for these two foci. Hemodynamic response in the supramarginal gyrus (-58, -46, 38) is greater during short-term scripts processing as compared to long-term ones, irrespective of the presentation modality. On the other hand, a focus of activation in the intraparietal sulcus (-52, -36, 38) show a differential profile of activation for long-term and short-term scripts according the two modalities. In this sulcus the contrasts of short term versus long-term is significant exclusively in the graphic modality. Foci of activation are represented here with red dots (located in the left hemisphere) in order to allow a more precise anatomical localisation.*

ascending posterior segment of
the parallel sulcus (-32, -34, 20)



angular gyrus
(-48, -64, 24)

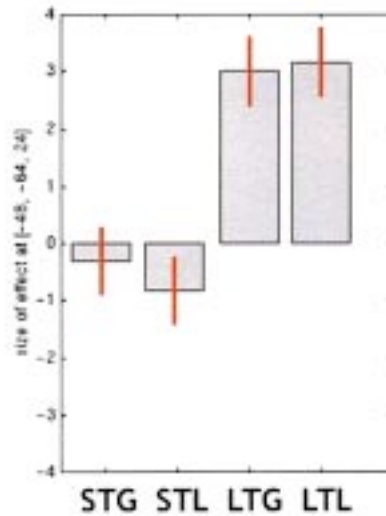
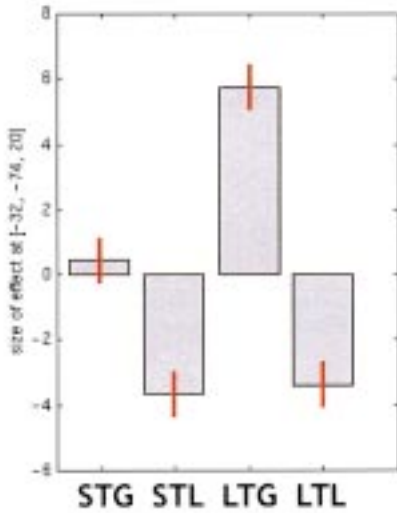
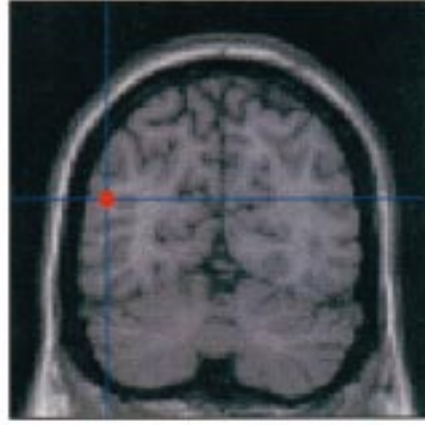


Fig. 5 – Anatomic-functional dissociation in the inferior posterior parietal cortex for long-term script planning in the two modalities. At the top of the figure, coronal sections of the brain show precise localization of peaks of activation in the angular gyrus and in the parallel sulcus. At the bottom post hoc analysis is presented for those two foci. The angular gyrus (-48, -64, 24) is more involved during processing long-term scripts as compared to short-term ones with no difference between the two presentation modalities. On the contrary the ascending posterior segment of the parallel sulcus (-32, -74, 20) shows a significant difference of activation between long-term and short term script processing exclusively in the graphic modality. This area is only involved in the graphic presentation and in this modality its response is stronger for long term scripts processing. Foci of activation are represented here with red dots (located in the left hemisphere) in order to allow a more precise anatomical localization.

Goal-directed behaviors, like those presented in our scripts, require predictions about events, internal states and actions that are likely to achieve a goal. To make these predictions, it is necessary to form associations between their internal representations. Neurophysiological studies in monkey have shown

that prefrontal neurons' activity reflect learned associative relationships between goal-relevant elements. Those neurons show conjunctive tuning for learned associations between cues, voluntary actions and reward. Prefrontal neurons even show tuning for complex behavior-guiding rules. It has been concluded that they may help form neuron ensembles that represent the regularities across experiences that describe the principles needed to achieve a particular goal in a particular situation (for a review see Miller, 2000). In human prefrontal areas are known to be involved in the storage and retrieval of the particular knowledge about the sequential aspects of planning. Patients with lesions in prefrontal cortex are impaired in planning the temporal order of series of actions in laboratory settings as well as in every-day life activities (Petrides and Milner, 1982; Shallice, 1988; Sirigu et al., 1995b, 1996; Goel et al., 1997). Neuroimaging studies have confirmed the involvement of this region in ordering scripts of action in healthy volunteers (Partiot et al., 1996; Crozier et al., 1999). These arguments lead us to suggest that in our study, the dorsolateral prefrontal activation is specifically associated with processing the sequential component of short-term script.

Short-term scripts processing was also associated with a strong activation in the inferior parietal cortex located in the supramarginal gyrus. Several neuroimaging experiments have demonstrated that the inferior parietal lobule is part of the network involved in motor representation (Decety et al., 1994; Stephan et al., 1995; Grafton et al., 1996; Rizzolatti et al., 1996; Decety et al., 1997; Krams et al., 1998; Grèzes and Decety, 2001). This region is known to participate in motor control by the encoding and the retrieval of motor sequence (Heilman et al., 1982; Rothi et al., 1985).

Short-term script planning can be considered as a means to involve the representation of transitive action. It has been shown that the mere observation of actions performed by others engage motor representations. For instance, a PET study by Grèzes et al. (1998) on healthy subjects has shown that the observation of pantomime of object-directed gestures (which belong to the short-term "action repertoire") in order to imitate them was associated with rCBF increase in the middle frontal gyrus, the SMA, the inferior and superior parietal lobe and the occipito-temporal junction. This is good evidence that regions involved in motor representations are also engaged in action observation. Some of these regions were also found to be engaged in script planning. Those arguments lead us to suggest that short-term actions may elicit a kind of motor imagery process, which could explain activation of some of the cortical regions involved in motor representation (i.e. supramarginal gyrus and the MT/V5 complex).

In humans, lesions in the posterior parietal cortex can lead to apraxia. This syndrome can be characterized by a failure in movement execution and movement representation (De Renzi, 1989; Sirigu et al., 1995a; Goldenberg, 1996; Ochipa et al., 1997). In the case of the so-called "modality specific" apraxia, the disorder is more salient when the movement has to be executed on verbal command as compared to when it is triggered by a visual cue. Heilman (1973) has indeed described the case of three patients who were unable to pantomime to command, but who were capable of pantomiming flawlessly when

presented with a tool or an object. Patients were also able to imitate correctly. The author termed this disorder “ideational apraxia” and proposed that the probable mechanism accounting for this impairment was a disconnection between the movement representation and the verbal system that interprets the command. Although the exact location of lesions that induce this defect remains unknown, based on the clinical presentation, Heilman suggested that the lesion was deep to the cortex in the region of the inferior parietal lobe. De Renzi et al. (1982) replicated Heilman’s observations and also described individuals who could not correctly gesture to visual stimuli but who correctly gesture to verbal command. This double dissociation suggests that two, at least partly, distinct brain networks are involved in processing visual and verbal stimuli for motor transformation.

We precisely found a dissociation in the parietal cortex between lexical and graphic modality for script processing. These results provide arguments for a neurophysiological explanation of the dissociations described above. A specific involvement of the intraparietal sulcus (IPS) was found in processing script of short-term action presented in the graphic modality, while the supramarginal gyrus is activated by short-term script irrespective of the presentation modality (Figure 4). The human anterior IPS has been proposed to participate in visually guided grasping (Binkofski et al., 1998). This area is likely the homologue of monkey AIP which contains neurons that respond to the visual and motor components of the grasp and that are tuned to specific shapes to be grasped (Sakata and Taira, 1994). In humans, IPS is also activated by tactile manipulation of objects, observation of hand movements and even passive viewing of graspable objects (for a review see Culham and Kanwisher, 2001). In our study IPS is involved in short-term scripts – which all illustrate actions requiring grasping – but only in the graphic modality. This is coherent with the idea that the IPS is specifically involved in visuomotor transformations, and not in “lexico-motor” transformations required by written language of the lexical scripts. In the light of our results it seems that the recall of a motor plan rely on a network which is modulated by the modality of the triggering stimuli (i.e. graphic or lexical).

The inferior parietal cortex has also been implicated in studies using verbal scripts (Partiot et al., 1996; Crozier et al., 1999). In the latter study, the authors showed that scripts processing elicited increased activity in the inferior parietal cortex, both in “BA 40” and in “BA 39”. However in their experiment, the scripts used were either short-term or long-term ones, both mixed in the experimental conditions. Our study was designed to differentiate scripts on the temporal contiguity between actions, which allowed us to demonstrate activation in the angular gyrus (Ba 40) for long-term scripts processing and in the supramarginal gyrus (Ba 39) for short-term scripts, respectively (Figures 4, 5). Thus, our results fit well with the hypothesis that the involvement of parietal cortex is influenced by the variation of the temporal contiguity between events that constitute a script. This is congruent with the role of the temporo-parietal associatives areas in action planning proposed in the introduction, which suggests that this region is involved in accessing knowledge required to assemble a plan. Interestingly, Harrington et al. (2000) have demonstrated that different patterns of activation in the left and right inferior parietal cortex were

associated with different finger sequences execution. The authors concluded that sequence might be encoded using different mnemonics, depending on the sequence-specific structure. In line with their hypothesis, we suggest that different areas within the inferior parietal cortex may subserve the encoding of different types of sequences.

Long-Term Action Planning

Processing scripts which describe long-term complex actions involved the angular gyrus, the precuneus, the medial part of the superior frontal gyrus bilaterally, and the inferior and middle temporal gyrus and the anterior cingulate gyrus on the left.

Long-term scripts processing requires, first of all, to understand the action described in the three events that are different in term of context, location and actor's attitude. The subjects had to infer the actor's goal and what was going on between each of these events at very distant points in time. The comprehension component might be then particularly salient in the case of long-term scripts. This could explain the presence of inferior and middle temporal activations that are likely to be related to script semantic processing. Several PET studies have reported involvement of the inferior and middle temporal gyri in the left hemisphere during semantic tasks (Demonet et al., 1992, 1994; Vandenberghe et al., 1996; Price, 1998). In addition, middle temporal activation has already been detected in a PET study using verbal scripts (Partiot et al., 1996).

The medial frontal activation could be related to an attribution of intention process. This hypothesis fits well with the results of several imaging studies dealing with theory of mind which have consistently demonstrated an involvement of the medial frontal cortex during tasks requiring mind-reading (Fletcher et al., 1995; Goel et al., 1995; Brunet et al., 2000; Gallagher et al., 2000). Scripts representing long-term action may well trigger a sort of attribution of intention-like process (a covert "mind reading" task). Indeed, understanding the aim of the actor might be especially helpful in order to judge whether a long-term action presented within a script is in the correct order. Long-term script processing requires the linking together of three events that are very different from each other. In order to cope with that, subjects may need to infer the actor's intention. On the other hand, short-term script ordering requires such type of processing to a lesser extent since all events are very close to each other and placed within the same "perceptual" context. In this case the intention of the actor is perhaps more directly appraised.

Long-term scripts recruited the angular gyrus, and as explained above this region is hypothesized to be specifically involved in long term sequences retrieval. Interestingly we found in this region the same kind of dissociation as that found for short-term scripts in the anterior inferior parietal lobe. In the angular gyrus, a peak of activation in the parallel sulcus shows a differential profile according to the presentation modality (Figure 5). In this very region, the comparison between long-term and short-term scripts led to significant rCBF increases only for the graphic presentation. This region within the parallel sulcus turns out to be, as the IPS, specifically involved in visuomotor transformation.

Thus, it seems that specific cortical areas in the parietal sulci are involved for visual stimuli processing in addition to the shared network detected for the two modalities of scripts presentation.

In the frontal lobe, the dorsolateral prefrontal cortex (DLPFC) wasn't found to be activated, although this region has been proposed to be particularly involved in sequence processing. This may be explained by its greater involvement in short-term script processing and therefore the subtraction design cancels out this activation. Interestingly, instead, the anterior cingulate gyrus was found to be specifically involved in long-term planning. In a review focussing on the human prefrontal cortex, Smith and Jonides (1999) have presented a body of results demonstrating that active manipulation of stored information (e.g. selective attention and task management) activates the anterior cingulate and the DLPFC. In our study, sequence processing requires active manipulation of stored information, whose retrieval is triggered by scripts. Anterior cingulate cortex may be predominantly involved in the manipulation of information in the case of long-term scripts processing.

Involvement of MT/V5 in Processing Static Stimuli

Unexpectedly, an activation was found in the occipito-temporal junction, in the MT/V5 complex, during processing graphic scripts although all the stimuli were static images. This region was also more activated for short-term scripts as compared to long-term ones regardless of the modality used (Figure 6). MT/V5 complex is known to process visual motion (Zeki et al., 1991; Watson et al., 1993; Tootell et al., 1995b). However, involvement of this region has been reported in cognitive tasks that do not involve an overt perception of motion, such as motion illusion (Zeki et al., 1993), motion after effect (Tootell et al., 1995a), motion imagery (Cohen et al., 1996; Goebel et al., 1998), and apparent motion (Goebel et al., 1998; Stevens et al., 2000). Motion perception might here be covert, since no explicit evocation of motion in the stimuli or in the instructions was given. Consistent with this idea a recent study has demonstrated that watching static images showing a moving actor involved MT/V5 as compared to images showing static postures (Kourtzi and Kanwisher, 2000). Hence, we suggest that the drawing-like presentation elicits, at an implicit level, visual dynamics between the different steps of action suggested by scripts. Perception of drawings illustrating action seems to activate the visual representation of a feature inseparable from action, that is motion. Thus, this region seems to participate not strictly in motion perception but more broadly in motion representation.

CONCLUSION

This study allowed us to explore the respective involvement of frontal and parietal cortices in implicit action planning by means of script ordering. Our results support the notion that two distinct frontal-parietal networks are engaged in short-term and long-term script processing. In addition, our study demonstrates two kinds of dissociations in the parietal lobe. A macro-

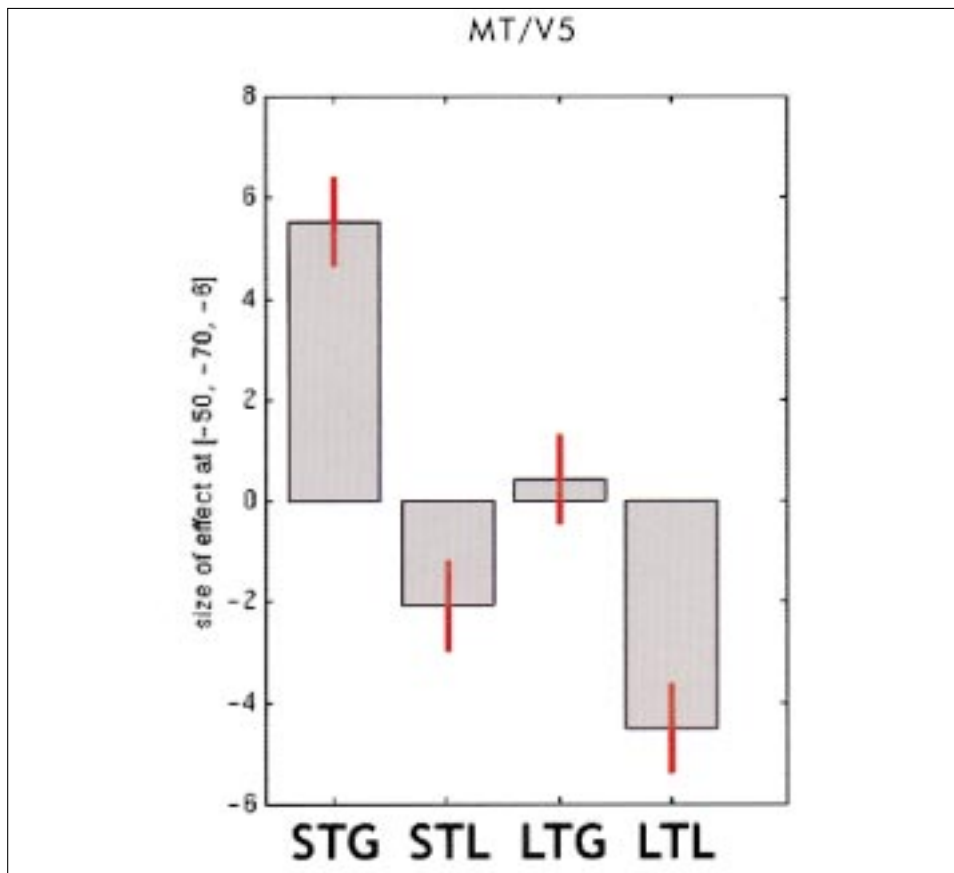


Fig. 6 – Post hoc exploration of a voxel belonging to the middle occipital gyrus (MT/V5) $x = -0$, $y = -70$, $z = -6$. The profile of activity illustrates the adjusted rCBF values in each experimental condition. This region is more activated during the graphic conditions as compared to the lexical ones and also more activated during short-term scripts processing as compared to long-term scripts processing.

dissociation between the anterior and the posterior portion of the inferior parietal lobe was found which accounts for processing short-term and long-term scripts respectively, as well as a micro-dissociation in each of these regions which is related to distinct processing depending on the presentation modalities. These results may help to better understand, at the neurophysiological level, apraxia which is a complex neurological syndrome still poorly understood.

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APPENDIX

List of Actions Depicted in the Four Scripts Conditions

LTG: travelling in a train, taking holiday pictures, making wine, buying a birthday present, growing apples, preparing a picnic, growing wheat, going fishing, inviting friends for dinner, making butter, scheduling a flight, stealing jewels, ordering a dress from a catalogue, going to funerals, taking children to and picking them up from school, looking for an apartment to rent, writing a scientific article, meeting someone and getting married, helping to deliver a calf, distilling spirits.

STG: washing dishes, preparing toast, making a sand castle, washing a salad, putting some sun cream on the beach, sitting and play the piano, breaking and beating eggs, driving out of the garage, brushing teeth, having a coffee from a machine, making a fire in a fireplace, paying with a check, putting on socks and shoes, entering a room and closing the door, receiving a phone call, blowing your nose in a handkerchief, smoking a cigarette, making a pancake, washing hair, taking a lift.

LTL: learning to drive, passing an exam, having a baby, looking for a job, breeding cows, standing trial, going on strike, writing and publishing a book, becoming a singer, making cheese, writing a law, making a movie, making an invention, discovering a new medicine, saving money, taking an A level examination, growing tobacco, making dresses, going to the doctor, making bread.

STL: slicing a roast, drinking water, taking a shower, writing a letter, withdrawing money, making coffee, shaving, washing strawberries, opening a bottle, washing the dishes in the washing machine, planting a seed, washing clothes, cooking potatoes, buying bread, drinking beer, eating an orange, taking a photo, hoovering, starting the car, swimming.