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The Left Intraparietal Sulcus Modulates the Selection of Low Salient Stimuli

Carmel Mevorach¹, Lilach Shalev², Harriet A. Allen¹,
and Glyn W. Humphreys¹

Abstract

■ Neuropsychological and functional imaging studies have suggested a general right hemisphere advantage for processing global visual information and a left hemisphere advantage for processing local information. In contrast, a recent transcranial magnetic stimulation study [Mevorach, C., Humphreys, G. W., & Shalev, L. Opposite biases in salience-based selection for the left and right posterior parietal cortex. *Nature Neuroscience*, 9, 740–742, 2006b] demonstrated that functional lateralization of selection in the parietal cortices on the basis of the relative salience of stimuli might provide an alternative explanation for previous results. In the present study, we applied a whole-brain analysis of the functional magnetic resonance signal when participants responded to either the local or the global levels of hierarchical figures. The task (re-

spond to local or global) was crossed with the saliency of the target level (local salient, global salient) to provide, for the first time, a direct contrast between brain activation related to the stimulus level and that related to relative saliency. We found evidence for lateralization of salience-based selection but not for selection based on the level of processing. Activation along the left intraparietal sulcus (IPS) was found when a low saliency stimulus had to be selected irrespective of its level. A control task showed that this was not simply an effect of task difficulty. The data suggest a specific role for regions along the left IPS in salience-based selection, supporting the argument that previous reports of lateralized responses to local and global stimuli were contaminated by effects of saliency. ■

INTRODUCTION

An important aspect of visual attention is the flexible capacity to prioritize external information for processing. Through this capacity, the human brain can process the same external information differently on different occasions, according to the current behavioral goals. A common laboratory example of the flexibility of attention is the global/local task (Navon, 1977), in which participants are able to attend to different levels of a hierarchical object, on one occasion responding to the local elements making up a global shape, while, under other task instructions, responding to the global shape (see Figure 1). However, there are asymmetries in the ease with which different stimulus properties are selected. Thus, in the global/local task, it is often easier for participants to attend to the global shape and to ignore the local elements, relative to when they have to attend to the local elements and ignore the global shape (Navon, 1977). Such differences may reflect variation in the bottom-up saliency of the stimuli for the visual system.

In recent years, considerable neurobiological evidence has accumulated indicating that flexible visual selection

is controlled by a fronto-parietal network within the brain (see Corbetta & Shulman, 2002; Kanwisher & Wojciulik, 2000 for reviews). In particular, the posterior parietal cortex (PPC) has been specifically implicated both when spatial selection is required (Nobre, Coull, Walsh, & Frith, 2003; Corbetta, Shulman, Miezin, & Petersen, 1995; Corbetta, Miezin, Shulman, & Petersen, 1993; Posner, Walker, Friedrich, & Rafal, 1984) and when selection is nonspatial (Wojciulik & Kanwisher, 1999; Humphreys, Romani, Olson, Riddoch, & Duncan, 1994). Thus, the PPC appears to be involved not only in directing attention to spatial locations but also in implementing selection using nonspatial properties of stimuli. One nonspatial aspect of selection may involve biasing attention on the basis of the relative saliency of stimuli. In the global/local task, for instance, the global shape cannot be attended spatially without the local elements also falling within the same “attentional window” (cf. Heinke & Humphreys, 2003). Here selection of the global shape may operate according to its greater saliency, even if both local and global elements are attended spatially. In contrast, selection of the local elements may, in such cases, be consequent on a bias favoring the less salient stimulus.

Evidence indicating that the PPC is involved in selection on the basis of saliency comes from recent studies

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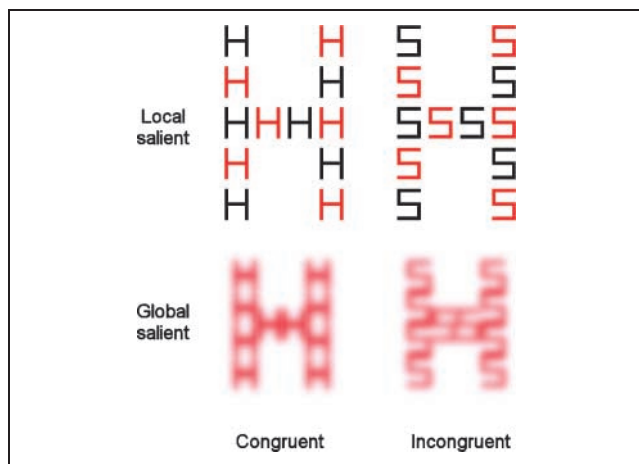


Figure 1. Examples of stimuli for the global/local task. Two display sets were used to achieve local saliency (upper pair) and global saliency (lower pair). The compound letters are displayed here on a white background, whereas in the actual experiment we used a black background.

in our laboratory. Using variants of the classic global/local task, we manipulated the saliency of the local and global stimuli by (for example) introducing a local contrast difference between some of the local elements or blurring the overall stimulus (emphasizing the saliency of the local and global forms, respectively; see also Lamb & Robertson, 1988; Martin, 1979). Patients with left parietal damage were highly susceptible to interference from the more salient stimulus level but, crucially, it did not matter whether the more salient stimulus was at the global or local level (Mevorach, Humphreys, & Shalev, 2006a). Converging evidence came from a study using repetitive transcranial magnetic stimulation (rTMS) over the left and right PPC of healthy participants (Mevorach, Humphreys, & Shalev, 2006b). A 2×2 design was used, in which the task that participants performed (attend to the global or the local forms) was crossed with which level in the display was the more salient. rTMS over the left PPC made it harder to respond to the less salient level and to ignore information on the more salient level, replicating the earlier neuropsychological data. Furthermore, rTMS over the right PPC had the opposite effect; in this condition, it became harder to select the more salient level and to ignore the less salient level. This result occurred irrespective of whether the local or global stimuli were the most salient.

These neuropsychological and rTMS data are consistent with neurophysiological results demonstrating that stimulus saliency is represented in the PPC (Constantinidis & Steinmetz, 2001; Gottlieb, Kusunoki, & Goldberg, 1998). These studies have systematically demonstrated that neurons in the PPC (area 7b and lateral intraparietal area) represent and encode the location of salient objects in a monkey's visual field. Recently, it has additionally been shown that these neurons can be biased to reduce their sensitivity to visually salient objects that are

known in advance to be irrelevant (Ipata, Gee, Gottlieb, Bisley, & Goldberg, 2006). Taken together, these findings indicate that neurons in the parietal cortex can be both biased toward and against saliency.

The view that variations in saliency are critical to the brain's response to hierarchical stimuli runs against the more standard view, that responses to hierarchical stimuli are determined by lateralized brain regions activated selectively by local and global properties of form. Thus, patients with left hemisphere lesions (often focused on the superior temporal–inferior parietal region) frequently have difficulty in responding to local shape (Lamb, Robertson, & Knight, 1990; Robertson, Lamb, & Knight, 1988; although see Mevorach et al., 2006a). In contrast, patients with lesions to homologous regions in the right hemisphere are impaired at responding to global forms (Lamb et al., 1990; Robertson et al., 1988). These results are supported to some degree by functional imaging studies, where selective activation has been reported in the left hemisphere for local element processing and in the right hemisphere for global shape processing (albeit in the ventral occipital cortex; Fink, Halligan, et al., 1997; Fink et al., 1996). Similarly, ERP studies indicate left activation for local shape tasks and increased right hemisphere activation for tasks that require discrimination of global form (Evans, Shedden, Hevenor, & Hahn, 2000; Proverbio, Minniti, & Zani, 1998; Heinze & Munte, 1993). Thus, any localization in neural responses to respectively high and low saliency stimuli may also couple with some degree of hemispheric specialization involved in processing local and global form, although this is difficult to judge because the task (respond local or global) often covaries with the saliency of the level of form (e.g., local being low salient and global high salient; although see Fink, Marshall, Halligan, & Dolan, 1999 for a different view).

These possibilities were evaluated here in Experiment 1, where we used fMRI to examine the relative influences of saliency and level of form, in the neural response to hierarchical forms. To do this, we orthogonally manipulated the task (respond to the local or global form) with the saliency of the level of the relevant form, using stimuli that had either local elements that were more salient than the global form, or global shapes more salient than the local elements. Compound letters were used and saliency was manipulated by introducing some color singletons within the local elements making up the global shape (increasing local saliency) or by blurring the overall shape (increasing global saliency; see Figure 1). This orthogonal manipulation allowed us to assess separately the brain regions associated with the main effect of saliency (respond to the form with high or low saliency) and those associated with the task (respond to the local or global form). However, as saliency manipulations would imply (by definition) differences in difficulty (typically expressed by longer reaction times), in Experiment 2 we conducted a control study where we varied the difficulty of

perceptual discrimination without varying the difficulty of attentional selection. This was done in order to assess whether the brain regions associated with the selection of low salient stimuli (in Experiment 1) were simply reflecting task difficulty.

EXPERIMENT 1: GLOBAL/LOCAL TASK

Methods

Subjects

Twelve participants¹ (5 women; mean age = 28 years) with normal or corrected-to-normal vision gave informed consent and participated in the study. Participants who normally use glasses for correction were fitted with MRI-compatible goggles replacing their glasses. The study was approved by the institutional ethics committee.

Stimuli

Two sets of displays were used in the global/local task to represent high global saliency and high local saliency and were presented on a black background.

For the condition with relatively high local saliency, the compound stimuli were created from orthogonal combinations of the letters H and S. Each compound contained both red and white local letters (see Figure 1). Each local letter subtended $1.34^\circ \times 1.76^\circ$ of visual angle (in width and height, respectively) and the global letter subtended $6.7^\circ \times 10.81^\circ$ of visual angle (in width and height, respectively). The interelement distance was 0.46° .

In the condition with relatively high global saliency, the compound letters were composed of the letters H and S, which were again combined orthogonally at the local and global levels. All the local letters were red. Each local letter subtended $1.34^\circ \times 1.76^\circ$ of visual angle (in width and height, respectively) and the global letter subtended $5.83^\circ \times 9.22^\circ$ of visual angle (in width and height, respectively). The interelement distance was 0.15° . These letters underwent a blur procedure in Paint Shop Pro 7.0 with a factor of 7.

The compound letters could appear at one of three possible locations at either the centre of the screen or 13.16° to the left or right of the fixation along the midline, which was done to ensure that participants performed the task under conditions encouraging diffuse attention. However, to minimize acuity effects and spatial shifting of attention, only those trials with centrally presented compound letter were analyzed. A white cross (0.57°) served as fixation and was presented in the center of the screen.

Experimental Procedure

The stimuli were projected onto a screen approximately 620 mm from the participant's eyes and viewed by a mirror mounted on the head coil. On different blocks of 32 trials participants were asked to identify the global or

the local elements of the compound letter while ignoring information on the other level. On half of the trials the compound figures consisted of the same global and local elements (congruent trials) and on the other half there were different global and local elements (incongruent trials). Each experimental trial started with the presentation of the fixation cross for 2000 msec followed by the target compound letter which was presented for 150 msec and was followed by a 1850-msec response interval. Participants were required to make a speeded response to the identity of the letter on the target level (H or S) by pressing one of two response keys on a keypad they held in their right hand. Each run of the task (a scan) included four blocks (two with "global" targets and two with "local" targets). A written instruction ("global task" or "local task") appeared at the center of the screen 2 sec prior to the beginning of each block. A variable intertrial interval was used (4–8 sec from the onset of a target compound letter in one trial to the onset of the target letter in the next trial). The first two blocks and the last two blocks of each scan were both either global more salient displays or local more salient displays (the order was counterbalanced between subjects and scans). Each such pair of blocks consisted of a global and a local block. The order of the global and local blocks was counterbalanced between participants. Each participant completed three scans. Prior to the scanning sessions, participants completed a practice run outside the scanner consisting of four 16-trial blocks.

fMRI Parameters

Images were acquired on a Philips 3-T Acheiva using the SENSE head coil. Functional images acquired using an echo-planar sequence (EPI) with 33 transverse 3 mm slices (voxel size 3 mm \times 3 mm \times 3 mm, TR = 2000 msec, TE = 35 msec, flip angle = 87° , field of view = 240 mm, sense factor = 2, 424 volumes were acquired in each scan). Five dummy scans were acquired prior to data recording. A high-resolution T1-weighted anatomical scan was also acquired in the same session as the function data with 175 sagittal slices, resolution 1 mm \times 1 mm \times 1 mm (TR = 8.4, TE = 38, flip angle = 8°).

fMRI Preprocessing and Analysis

The analysis was carried out using FEAT (FMRI Expert Analysis Tool) Version 5.4, part of FSL (FMRIB's Software Library; www.fmrib.ox.ac.uk/fsl). Time-series statistical analysis was carried out using FILM (FMRIB's Improved Linear Model) with local autocorrelation correction (Woolrich, Ripley, Brady, & Smith, 2001). The first 6 volumes of each scan (12 sec) were removed to reduce the transient effects of magnetic saturation and to allow the hemodynamic response to stabilize. Individual scans were preprocessed in the following ways before further analysis. Slice-timing correction (using Fourier-space

time-series phase-shifting) was applied. Movements of the participants head were corrected for using MCFLIRT (motion correction with FMRIB's linear registration tool; Jenkinson, Bannister, Brady, & Smith, 2002). Average head movement by participants was low—0.51 mm (range: 0.24–0.97 mm). The skull and other nonbrain matter were removed using BET (Brain extraction tool; Smith, 2002). Images were then spatially smoothed using a Gaussian kernel of FWHM 5 mm and all volumes within a scan were mean-based intensity normalized using the grand mean for the time series. Signals within the scan were then high-pass temporal filtered (Gaussian-weighted LSF (least squares fit) straight-line fitting, with $\sigma = 50.0$ sec). Each participants' whole-head EPI image was registered to their individual (brain extracted) structural images. The individual scans were then registered to high-resolution standard images in MNI space using FLIRT (Jenkinson et al., 2002; Jenkinson & Smith, 2001).

The study had an event-related design with an event being defined as the 2-sec period starting from the presentation of a hierarchical letter. Higher-level analysis was carried out using FLAME (FMRIB's local analysis of mixed effects; Woolrich, Behrens, Beckmann, Jenkinson, & Smith, 2004; Beckmann, Jenkinson, & Smith, 2003). Z (Gaussianized T/F) statistic images were thresholded using clusters determined by $Z > 2.3$ and a (corrected) cluster significance threshold of $p = .05$ (Worsley, Evans, Marrett, & Neelin, 1992).

The BOLD signal (expressed as percent change) was extracted for all voxels contained within a cluster of significant activation found during the condition in which there was a salient irrelevant distractor compared to a salient relevant target on the group level (left intraparietal sulcus [IPS]; see Results). For each participant, the BOLD signal was averaged across all voxels in the cluster as a function of the experimental condition. These data were then analyzed using an ANOVA with saliency (global salient and local salient) and task (local and global) as within-subject factors. In addition to these analyses, we evaluated whether there was a relation between behavior and activation in the left hemisphere regions that increased activation with high relative to low saliency distractors. To do this, we examined the correlation across subjects between the slowing of RTs with salient distractors relative to salient targets with the difference in BOLD signal in the left IPS cluster.

Results and Discussion

Behavioral Responses

Behavioral data were collected during the scanning sessions (see Methods). A repeated measures ANOVA was carried out on participants' RTs with saliency (global-salient vs. local-salient), target level (global vs. local), and congruency (congruent vs. incongruent) as within-subject factors. Congruent displays were identified faster than incongruent ones [606 and 655 msec for congruent

and incongruent displays, respectively; $F(1, 9) = 15.324$, $p < .005$]. Furthermore, a significant interaction of saliency and target level [$F(1, 9) = 18.262$, $p < .005$] indicated that the pattern of performance reversed under the two saliency conditions (Figure 2). For the global salient condition, performance was faster for global compared with local targets [581 and 672 msec for global and local identification, respectively; $t(9) = 5.24$, $p < .001$], whereas for the local salient condition, performance was slower for global relative to local targets [670 and 601 msec for global and local identification, respectively; $t(9) = 2.809$, $p < .01$]. These data confirm that relative saliency was reversed for the two different saliency conditions. In contrast to the evidence on variations in saliency based on global and local precedence effects, the pattern of interference effects (incongruent–congruent conditions) was not significantly changed under the two saliency conditions [$F(1, 9) = 2.207$, $p = .172$]. This suggests that the effects of saliency on stimulus selection may, to some degree, be distinct from effects on response selection.

A similar ANOVA carried out on accuracy rates revealed a main effect of congruency [$F(1, 9) = 5.643$, $p < .05$], with accuracy rates for congruent trials (99% correct) higher than the rates for incongruent trials (96% correct). No other effects reached significance.

Imaging Data

Brain activity time-locked to the individual trials was determined using an event-related analysis of the fMRI data (see Methods).

Effects of distractor saliency. To assess the neural correlates of attentional responses toward or away from

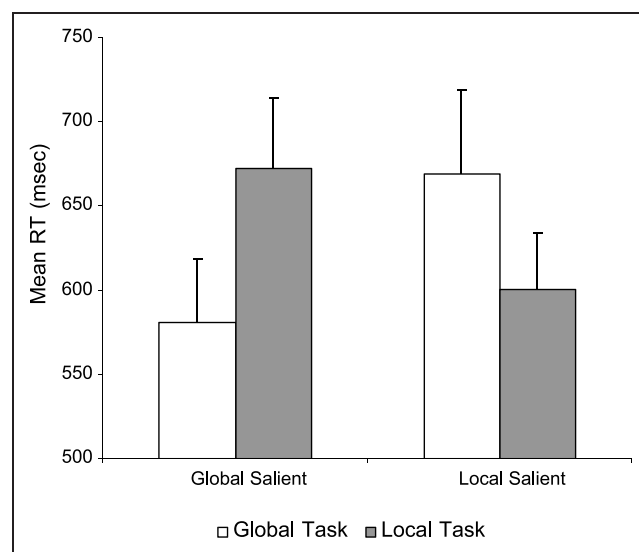


Figure 2. Behavioral performance in the global/local task. Mean RTs (\pm SEM) for the global and local letter identification as a function of saliency (global salient and local salient).

Figure 3. Activity related to the conditions where the distractor level was more salient (distractor-salient) versus where the target level was more salient (target-salient) ($n = 12$, $p < .05$, corrected). Activations are plotted on dorsal, left lateral, and transverse views (left, center, and right panels, respectively) of the mean normalized structural image of the 12 participants.



salient stimuli, we contrasted the experimental conditions in which the distractor level was more salient (distractor-salient) (i.e., the global task in the local-salient condition, and the local task in the global-salient condition) with the conditions in which the target level was more salient (target-salient) (i.e., the global task in the global-salient condition and the local task in the local-salient condition). Figure 3 shows areas of activity associated with the distractor level being more salient than the target level (see also Table 1 for the stereotactic locations of the peak voxels in these areas of activation). Responses under conditions of high distractor salience were associated with activation along the left IPS (mostly inferior bank), including the angular gyrus (AG), the superior parietal lobule (SPL), and the posterior segment of the supramarginal gyrus (SMG). In contrast, no unique activation was associated with salient target conditions (in the reverse contrast).

To confirm whether the left-lateralized activation for the distractor-salient (compared with the target-salient) conditions were elicited by a specific task (i.e., global or local task), we extracted the BOLD signal (denoted by percent change from a global mean) within the cluster of activation along the left IPS. This was done for each participant under each of the four experimental conditions (global task, global-salient; global task, local-salient; local task, global-salient; and local task, local-salient). An ANOVA with relative saliency (global-salient and local-salient) and task level (global and local) as within-subject factors revealed a significant interaction [$F(1, 11) = 13.443$, $p < .005$; see Figure 4]. Planned comparisons showed that, for voxels in the left IPS cluster, the BOLD signal change was significantly higher for the global task conducted under conditions of local salience (0.26% change) compared with global salience [0.17% change; $t(11) = 2.392$, $p < .05$], and the same trend held for the local task under conditions of global salience (0.25% change) than under conditions of local-salience [0.13% change; $t(11) = 2.043$, $p < .05$].

To further assess the relations between activation along the left IPS and the ease or difficulty with which participants were able to ignore the salient distractor level, we calculated the correlation coefficient between the difference in BOLD signal averaged across the voxels

in the left IPS cluster between the distractor-salient and target-salient conditions with the corresponding observed average RT difference for each individual. This revealed a significant positive relation between the difference in the BOLD signal change and the difference in RT for the left IPS cluster ($r = .66$, $p < .05^2$; see Figure 5). This finding indicates that the larger the difference in saliency for a participant (i.e., the greater the difference in RTs between the distractor-salient and target-salient conditions), the larger the difference in BOLD signal in the left IPS between the distractor-salient and target-salient conditions.

Local and global tasks. A second set of analyses evaluated activations associated with the global and local tasks. No areas were significantly more active for the local task in comparison to global tasks or for the global task compared with the local task. One possibility for this lack of lateralized activity in the brain may relate to the specific type of stimuli used here. Specifically, it may be argued that whereas in the local-salient displays the local elements contain high spatial frequency information and the global shape contains low spatial frequency information, in the global-salient displays (where the local elements are blurred) there is only low spatial frequency information available for both the local and

Table 1. Regions of Activation Associated with Distractor Saliency (vs. Target Saliency) and Global (vs. Local) Task under Local-salient Condition

Region	Side	x	y	z	Z Score	Cluster Size	p
<i>Distractor-salient > Target-salient</i>							
Angular gyrus (extending anteriorly)	L	-30	-68	34	3.02	831	.012
<i>Global > Local (Local-salient)</i>							
Supramarginal gyrus (extending posteriorly)	L	-46	-40	38	3.58	708	.002

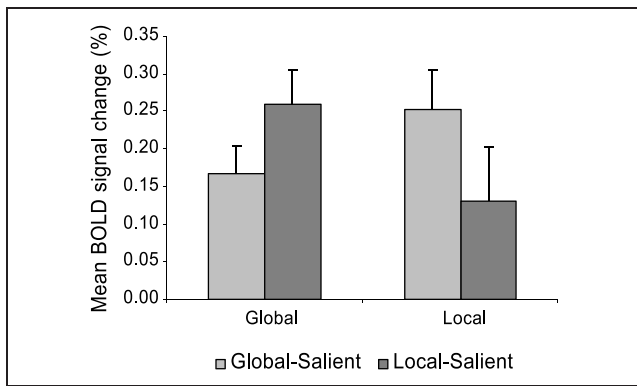


Figure 4. Activity in the left IPS for the different experimental conditions of the global/local task. Mean BOLD signal change, averaged across all voxels and across participants. Error bars denote interparticipant standard error.

global elements. Hence, left lateralization for local processing and right lateralization for global processing might only occur for the local-salient displays (if for instance, local and global processing are linked to high and low spatial frequency processing, respectively; see, for instance, Shulman, Sullivan, Gish, & Sakoda, 1986) but not for the global-salient displays. Therefore, pooling information across the different saliency conditions may obscure left- and right-lateralized activity for local and global processing in the local-salient displays. In order to test that suggestion, we contrasted activity linked to global and local processing specifically for the local-Salient condition. If this account holds, local processing should result in left-lateralized activation and global processing in right-lateralized activation. However, as can be seen in Table 1, this comparison revealed no unique activation for local compared with global task performance. Rather, global task performance resulted in left-lateralized activation (much like the overall analysis). This is in accord with our account of salience-

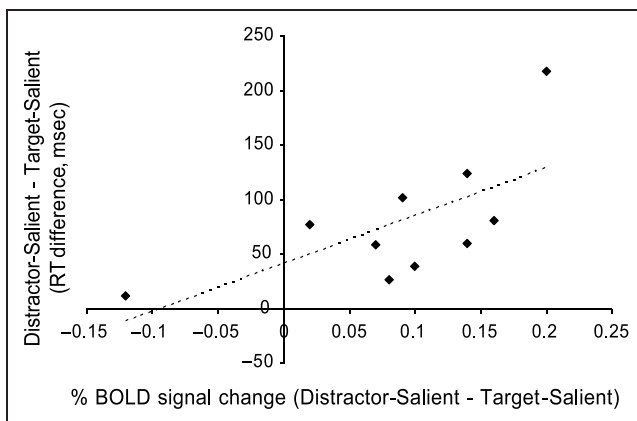


Figure 5. Correlation between the differences in BOLD signal change for distractor-salient and target-salient conditions and the corresponding differences in RTs for the left IPS cluster.

based selection (as global information is less salient than local in this condition).

EXPERIMENT 2: A CONTROL OF TASK DIFFICULTY

The present study has used an operational definition of saliency which relies on observed differences in RTs between the distractor-salient and target-salient conditions. As such, it is not clear whether the cluster of activation we found when distractors were salient (distractor-salient–target-salient conditions) reflects processes uniquely linked to salience-based selection or rather to general differences in task difficulty. Previous investigations of the relations between attentional selection and task difficulty (e.g., Wojciulik & Kanwisher, 1999) have demonstrated distinct regions within the parietal lobe linked to attentional demands (posterior IPS) and to task difficulty (the anterior, inferior parietal lobe). However, the left IPS cluster found here may span both regions. To test that task difficulty per se was not critical here, we examined whether the regions of left parietal lobe of current interest were also mediated by task difficulty (or RT differences) in a control task in which difficulty (but not salience selection) was manipulated.

Methods

Subjects

Twelve participants (including seven of the original participants from Experiment 1) took part in this study (3 men; mean age = 30 years). All had normal or corrected-to-normal vision and gave informed consent. The study was approved by the institutional ethics committee.

Stimuli

Black Landolt rings (1.37°) were used on a white background for the perceptual discrimination task. The rings were either solid or broken (see Figure 6). Broken rings had a gap (0.11° in width) located either at the very top or very bottom of the ring in line with its centre. These gaps were tilted (20°) to the right or left of the vertical.

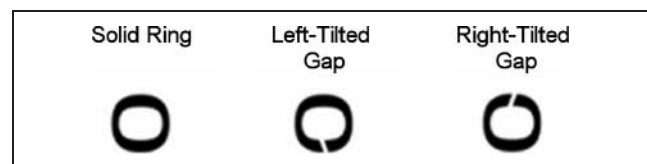


Figure 6. Examples of stimuli for the perceptual discrimination task. Landolt rings could have been either solid (left), broken with a left-tilted gap (middle), or right-tilted gap (right). The gaps could appear at the bottom or the top of the rings.

The rings could appear either 1.33° above or below the center of the screen along the vertical midline. Two black crosses (0.57°) served as fixation and were presented 2.86° to the left and right of the center of the screen.

Experimental Procedure

The stimuli were projected onto a screen approximately 620 mm from the participant's eyes and viewed by a mirror mounted on the head coil. Participants performed two tasks in alternating blocks. In the easy blocks, participants were required to make a speeded response to the presence/absence of the gap in the Landolt ring by pressing one of two response keys on a keypad they held in their right hand (index and second finger for gap and no-gap, respectively). In the hard blocks, judgments were made on the orientation of the gap (left-tilted or right-tilted) by pressing one of three response keys (index, second, and third fingers for left-tilted gap, no gap, and right-tilted gap, respectively). These tasks were selected from pilot studies so that the RT difference between the hard and easy trials was at least as large as the difference between distractor-salient and target-salient trials in Experiment 1. An instruction ("Easy task" or "Hard task") was presented in the center of the screen for 2 sec immediately before the beginning of each block. There were eight trials in each block and participants alternated between the two types of task block (hard and easy). Trial blocks were interspersed by fixation intervals (in which only the fixation crosses were visible). Half the trials of each block consisted of solid rings and the other half of broken rings (with a small gap). Each experimental trial started with the presentation of the fixation crosses for 2000 msec followed by the target Landolt ring, which was presented for 100 msec and was followed by a 1900-msec response interval. Each run of the task (a scan) included eight blocks (4 easy and 4 hard) which were interspersed with seven fixation (baseline) intervals. A constant inter-trial interval was used (4 sec from the onset of a target ring in one trial to the onset of the target ring in the next trial). Prior to the scanning, participants completed a practice run (outside the scanner) consisting of two easy and two hard blocks.

fMRI Parameters

Images were acquired on a Philips 3-T Acheiva using the SENSE head coil. Functional images acquired using an echo-planar sequence (EPI) with 33 transverse 3-mm slices (voxel size = $3\text{ mm} \times 3\text{ mm} \times 3\text{ mm}$, TR = 2000 msec, TE = 35 msec, flip angle = 87° , field of view = 240 mm, sense factor = 2, 190 volumes were acquired in each scan). Five dummy scans were acquired prior to data recording. Eight out of the 12 participants performed the task on a different session than the global/

local task. For those participants, a high-resolution T1-weighted anatomical scan was also acquired in the same session as the functional data with 175 sagittal slices, resolution $1\text{ mm} \times 1\text{ mm} \times 1\text{ mm}$ (TR = 8.4, TE = 38, flip angle = 8°). For the remaining four subjects who performed the task during the same session as the global/local task, no additional anatomical scan was acquired. Those subjects performed this control task following the completion of the previous global/local task.

fMRI Preprocessing and Analysis

Preprocessing and analysis were carried out in a similar manner to the main experiment, using FEAT (FMRI Expert Analysis Tool) Version 5.90, part of FSL (FMRIB's Software Library; www.fmrib.ox.ac.uk/fsl). As above, time-series statistical analysis was carried out using FILM (Woolrich et al., 2001). The first 6 volumes of each scan (12 sec) were removed. Before further analysis, slice-timing correction and corrections for head motion were applied. Average head movement by participants was low—0.20 mm (range: 0.05–0.37 mm). The skull and other nonbrain matter were removed using BET (Smith, 2002). Images were then spatially smoothed using a Gaussian kernel of FWHM 5 mm, and all volumes within a scan were mean-based intensity normalized. Signals within the scan were then high-pass temporal filtered (Gaussian-weighted LSF straight line fitting, with sigma = 46.0 sec). Each participants' whole-head EPI image was registered to their individual (brain extracted) structural images and a high-resolution standard image in MNI space using FLIRT (Jenkinson et al., 2002; Jenkinson & Smith, 2001).

The study had a block design with three types of blocks: fixation, easy, and hard. Each of the easy and hard blocks was 30 sec long and each of the fixation blocks was 16 sec long. The four easy and four hard blocks were alternated with the seven fixation blocks interspersed in between. For each participant, activation for the fixation blocks was subtracted from the activation in the easy and hard blocks. Higher-level analysis was carried out using FLAME (FMRIB's Local Analysis of Mixed Effects; Woolrich et al., 2004; Beckmann et al., 2003). Z (Gaussianized T/F) statistic images were thresholded using clusters determined by $Z > 2.3$ and a (corrected) cluster significance threshold of $p = .05$ (Worsley et al., 1992). In addition, for each participant, we also contrasted activation in the hard condition with the easy condition. For this contrast, Z (Gaussianized T/F) statistic images were thresholded at $p = .005$, uncorrected (Worsley et al., 1992). ROI analysis was carried out using the left IPS cluster of activation obtained in Experiment 1 (the global/local task). The BOLD signal (expressed as percent change) was extracted and averaged across all voxels contained within that cluster for each participant for the easy-fixation and hard-fixation contrasts.

Results and Discussion

Behavioral Responses

As expected, RTs for the easy blocks (593 msec) were significantly faster than RTs for the hard blocks [705 msec; $t(11) = 4.69, p < .001$]. Most important for our purposes, this difference in performance (112 msec) was no less than the difference in performance observed between the distractor-salient and target-salient conditions in the previous study (80 msec). Accuracy rates were relatively high and did not differ between the easy (96% correct) and hard (96% correct) blocks [$t(11) = 0.209, ns$].

Imaging Data

Brain activity was determined using a block-design analysis of the fMRI data (see Methods). Basic contrasts of easy task versus fixation revealed clusters of bilateral neuronal activity in the precentral gyrus and supplementary motor area (see Table 2 for the stereotactic locations of the peak voxels in these areas of activation). Activation was also found in the left inferior lateral occipital

cortex, the left SPL, and the SMG. For the contrast of hard task versus fixation, similar bilateral activity was found in the precentral gyrus as well as similar left parietal activity (SPL and SMG). In addition, cerebellar activity was also visible (Table 2). Comparing hard versus easy task conditions revealed activation in the right SMG, bilateral precentral gyrus, left central opercular cortex, right lingual gyrus, and cerebellum (Table 2). However, no left parietal activity was found.

Both easy and hard tasks activated a predictable network of frontal (likely to include the human frontal eye fields), parietal, and occipital regions, similar to that found in other visual attention tasks (Corbetta et al., 1998). Furthermore, our parietal and occipital regions also overlap with regions previously implicated in pattern discrimination (Faillenot, Sanaert, Van Hecke, & Orban, 2001). Areas that showed increased activation in the hard versus easy task might indicate brain regions involved in effort or load. Using a motion tracking task, Culham, Cavanagh, and Kanwisher (2001) found that activity in the precentral sulcus, the superior frontal sulcus, the supplementary motor area, and the anterior IPS

Table 2. Regions of Activation Associated with Easy and Hard (vs. Fixation) Tasks and for Hard vs. Easy

Region	Side	<i>x</i>	<i>y</i>	<i>z</i>	<i>Z</i> Score	Cluster Size	<i>p</i>
<i>Easy > Fixation</i>							
Precentral gyrus (extending medially to the superior frontal gyrus)	L	-46	-6	56	4.45	717	.003
Superior parietal lobule (extending to the posterior supramarginal gyrus)	L	-30	-50	42	3.94	703	.004
Supplementary motor area (bilaterally)	R	12	12	48	3.52	620	.008
Lateral occipital cortex	L	-44	-66	-10	3.72	548	.016
Precentral gyrus (extending medially)	R	42	-2	44	4.42	540	.017
<i>Hard > Fixation</i>							
Precentral gyrus (extending posteriorly to include the supramarginal gyrus and superior parietal lobule)	L	-42	-8	52	4.62	1779	.001
Cerebellum	L	-6	-78	-24	3.64	720	.005
Precentral gyrus	R	44	2	48	4.3	594	.015
Lateral occipital cortex (inferior)	L	-44	-64	-8	3.7	479	.045
<i>Hard > Easy</i>							
Supramarginal gyrus	R	34	-36	36	4.67		.005
Precentral gyrus	L	-32	-14	50	3.9		.005
Precentral gyrus	R	40	-6	50	3.84		.005
Lingual gyrus	R	36	-38	-8	3.98		.005
Central opercular cortex	L	-50	-18	20	3.86		.005
Cerebellum	R	12	-50	-24	3.65		.005

was modulated by task demands, whereas activity in the frontal eye fields and superior parietal lobe and visual areas related to the task was not. Although our results agree with their conclusions that there are both task-load- and non-task-load-related regions active for a task, our set of activations does not completely overlap with theirs, presumably reflecting the different tasks used. The differences in parietal and frontal activation, for instance, could be due to the different attentional demands (our task used a more relatively simple task likely dependent on focused attention, whereas their motion tracking task likely involved more distributed attention). The difference between task-based and load-based activity is a subject for further research, but distinct from our interests in how difficulty is modulated in the global/local task by stimulus saliency.

To assess whether activity in the left IPS in the previous study merely reflected task difficulty, we used the cluster of the left IPS obtained in Experiment 1 for ROI analysis in the current study. We extracted the BOLD signal (denoted by percent change from a global mean) within the cluster of activation in the left IPS for each participant under two conditions: easy-fix and hard-fix. We found no significant difference for activation in the hard (0.14%) compared with the easy (0.14%) conditions [$t(11) = 0.028, p = .489$]. Furthermore, we directly compared activation in the left IPS in the two experiments by subjecting the % BOLD signal change to an ANOVA with task (perceptual discrimination vs. global/local) as between-subject factor and difficulty (easy vs. hard³) as within-subject factor. A significant interaction of task and difficulty [$F(1, 23) = 5.936, p < .025$] revealed a clear difference in the effect difficulty had on activation within the left IPS under the two tasks (Figure 7A).

However, as not all of the participants performed both tasks, it might be the case that individual differences between the groups yield the different pattern of activation (especially as there were higher rates of female participants in Experiment 2 compared with Experiment 1). To control for that (albeit unlikely) option, we analyzed the BOLD signal change in the two tasks for only those seven participants that performed both tasks. An ANOVA with task (perceptual discrimination vs. global/local) and difficulty (easy vs. hard) as within-subject factors revealed a significant interaction of task and difficulty [$F(1, 6) = 13.692, p < .01$; see Figure 7B]. Again, this interaction supports the notion that whereas voxels in the left IPS showed greater activity for the distractor-salient compared with the target-salient conditions of the global/local task, no such difference was observed for the hard compared with the easy blocks of the perceptual discrimination task. Indeed, examination of the individual data in both tasks revealed that for the global/local task, all seven participants showed higher BOLD signal change in the distractor-salient compared with the target-salient conditions. However, only two

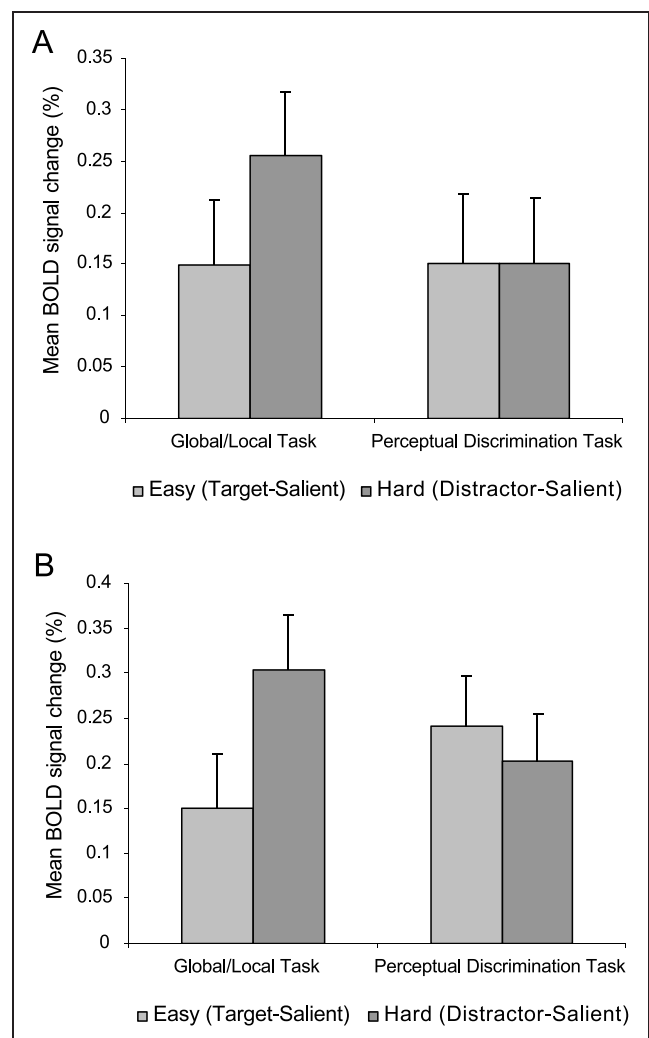


Figure 7. Activity in the left IPS for easy/target-salient and hard/distractor-salient conditions for the perceptual discrimination and global/local tasks. (A) Mean BOLD signal change, averaged across all voxels and across the two groups of 12 participants that performed each task. Error bars denote interparticipant standard error. (B) Mean BOLD signal change, averaged across all voxels and across the seven participants that performed both tasks. Error bars denote interparticipant standard error.

participants showed higher activation for the hard compared with the easy conditions of the difficulty task (while the other five showed the reverse pattern).

Activation in the left IPS area found in the global/local task does not appear to be modulated by task difficulty in any general sense, only distractor saliency. Thus, the difference in activation observed in the global/local task cannot simply be attributed to differences in difficulty (expressed by RT) between the task conditions.

GENERAL DISCUSSION

We examined the neural activation related to the saliency and level of stimulus representations mediating responses to hierarchical stimuli. The data demonstrate clear effects

of saliency, with activation in the left IPS associated with responses to low saliency stimuli in the presence of higher saliency distractor information. This result held both when responses were made to local elements (under conditions of high global saliency) and to global forms (under conditions of high local saliency). In contrast, there was no activation associated with the level of representation required for the task.

Effects of Saliency

The results indicating left IPS activation when stimuli low in salience have to be selected in the presence of high saliency distractors fit with the evidence from rTMS reported by Mevorach et al. (2006b). They found that rTMS to the left PPC disrupted responses to low saliency targets occurring with high saliency distractors; here we found unique activation along the left IPS when participants were asked to ignore information from the more salient level of a hierarchical letter figure. In addition, an ROI analysis revealed that this activation was not related to whether the local or the global stimulus was salient, nor to whether the task required local or global forms to be identified. Left IPS activation also correlated with the RT difference between responses when the target had low relative to high saliency. This suggests that there was increased activity in the left IPS in participants who experienced a particularly pronounced effect of low saliency targets (who were most slowed when responding to low relative to high saliency stimuli). This may suggest that neurons in the left IPS are recruited when participants experience a substantial difference in the relative saliency of distractors and target in order to enable accurate selection of the target level. Although a significant correlation does not indicate causal relation between the left IPS and responding to low saliency targets, the data do converge with prior rTMS results (Mevorach et al., 2006b) to indicate that the left IPS plays a necessary role in visual selection under these conditions.

It is also the case, however, that it is more difficult to respond to low relative to high saliency targets (which results with slowing of the responses), especially when distractors are salient. Hence, any activation specifically linked to the selection of low saliency targets here could potentially be attributed to stronger recruitment of brain regions when the task is more demanding or simply to longer response processes taking place. In order to evaluate this suggestion, we conducted a control experiment in which task difficulty was manipulated while the demands on visual selection remained constant. A whole-brain analysis and, specifically, an ROI analysis over the left IPS cluster revealed a critical difference in the pattern of activation for the global/local task (Experiment 1) and the perceptual discrimination control task (Experiment 2). Although in the two tasks there were equal effects of task difficulty on performance, only the

global/local task generated differences in BOLD signal in the left IPS. The difference in activation patterns across the tasks cannot be attributed to a difference in the magnitude of the difficulty effect, as this effect was, if anything, larger for the perceptual discrimination task. Furthermore, the contrasting pattern of activation for the two tasks could not be attributed to the different stimuli that were used as the critical contrasts (i.e., between high and low saliency levels in Experiment 1, and between the easy and difficult discriminations, in Experiment 2) subtract out effects due to the specific stimulus (constant for each contrast). Hence, any stimulus-specific effects should be removed when we compare the saliency effect in Experiment 1 and the difficulty effect in Experiment 2. This suggests that activation in the left IPS was specifically linked to the selection of stimuli that have low salience in the presence of high-salient distractors, and not to general demands linked to increases in task difficulty. The latter case has been previously shown to be linked to robust activation in the prefrontal cortex (Duncan & Owen, 2000). For many different task demands, there is a similar recruitment of the mid-dorsolateral, mid-ventrolateral, and dorsal anterior cingulate cortex. Clearly, the activation we report in the left IPS associated with changes in perceptual saliency does not generate this pattern.

In the present study, there was activation for low relative to high saliency stimuli across a cluster of neurons spanning both posterior and anterior parts of the IPS. However, the IPS has previously tended to demonstrate functional separation roughly corresponding to a spatial segmentation along the anterior–posterior axis (e.g., Rice, Tunik, & Grafton, 2006; Rushworth, Ellison, & Walsh, 2001; Rushworth, Krams, & Passingham, 2001; see also Cavada & Goldman-Rakic, 1989a, 1989b, for functional and structural segmentation of the IPS homologue in monkeys). Furthermore, functional specificity has been also reported with respect to the AG and the SMG (both featuring in our cluster of activation) as well as with their lateralization (e.g., Chambers, Payne, Stokes, & Mattingley, 2004 for the right AG in attentional orienting and Rushworth, Ellison, et al., 2001; Rushworth, Krams, et al., 2001 for the left SMG in motor attention). Indeed, it is a question for future research whether the activity we show here represents more than one mechanism or function. It might be the case, for instance, that more posterior aspects of the left IPS (including the AG) are critical to the attentional selection process, whereas more anterior aspects (including the SMG) are more involved with the motor response selection process.

Other studies have also found evidence of functional segmentation and lateralization in the parietal cortex. For instance, Wojciulik and Kanwisher (1999) contrasted BOLD activation for spatial and nonspatial selection tasks within the same participants and found a dissociation between the SPL and the lateral IPS/inferior parietal lobule (IPL), with these areas linked to spatial and

nonspatial attention, respectively. The current findings fit with this proposal, with the left IPS being implicated when selection is based on a nonspatial property—stimulus saliency. The finding of left-lateralized IPS activation for saliency-based selection also corresponds with Coull and Nobre (1998), who identified the left IPS/IPL as more relevant to nonspatial (temporal) selection than to spatial orienting.

We failed to find evidence for activation of the right PPC when responses were made to a salient stimulus in the presence of a low saliency distractor. In contrast to this, Mevorach et al. (2006b) reported that rTMS to the right PPC disrupted responses to high saliency stimuli. Our failure to isolate activation in the high saliency conditions here may reflect some of the limitations in fMRI, relative to an interventionist technique such as TMS. For example, responses to high saliency stimuli are (by definition) easier than those to low salient items, and this makes it difficult to show selective activation given that activation is often increased under more demanding conditions. In addition, it is possible that there is some right PPC involvement in all of the present conditions, if this brain region responds to all salient stimuli irrespective of their task relevance. Corbetta and Shulman (2002), for example, have argued for a role of the right ventral fronto-parietal network in “saliency detection,” acting as a “circuit breaker” to current tasks, even if the salient information is task irrelevant. There is also behavioral evidence for irrelevant but salient stimuli competing for selection with task-relevant items (Theeuwes & Burger, 1998), and we may speculate that this competition is mediated through the right PPC. If this is the case, then the right PPC might be recruited by salient distractor as well as target information in the current study, and so is involved even when the task requires selection of the low salient stimuli due to the presence of the highly salient distractor.

Previous imaging studies focusing on global/local processing have not manipulated the relative saliency of the global and local levels explicitly. One exception is a study by Fink et al. (1999), in which PET was used to evaluate brain activity when subjects performed a global/local task while the relative spatial frequency of the compound figures was varied. Fink et al. reported that there was lateralized brain activity in posterior brain regions according to the target level, across the spatial frequencies sampled (e.g., left hemisphere activation to local and right hemisphere to global targets). However, the spatial frequency manipulation used did not reverse the relative saliency of the two levels (a main effect of level was reported where, overall, the global level was responded to significantly faster than the local level; Fink et al., 1999). This result, then, remains consistent with the finding we report here, where left PPC activity was linked to responding to a low saliency stimulus. We contend that, to separate saliency and level, the conditions must generate crossover effects in performance, as we have shown.

Effects of Task

Although we found effects of saliency on neural activity, we found no overall effects of the task (respond to the local or global form) and obviously no lateralization of responses to local and global stimuli. Previous imaging findings are inconsistent with respect to the effects of local and global tasks on neural activity. Some studies have clearly shown lateralized effects (e.g., local task—left hemisphere; global task—right hemisphere; Lux et al., 2004; Han et al., 2002; Fink et al., 1999), whereas others have not (e.g., Sasaki et al., 2001; Martinez et al., 1997), and some have even shown a reversal of the “normal” lateralization of functions (Fink, Marshall, et al., 1997). One possible explanation for the overall lack of task lateralization in the present study is the use of two different sets of displays (implementing the manipulation of the relative saliency of the local and global levels of form). It is quite possible that the local and global tasks recruited different processes under the local salient and global salient conditions as the visual input under these two conditions differed. Indeed, an account that stresses spatial-frequency processes may suggest that only in the local-salient displays was both high and low spatial frequency information available (linked with local and global processing). However, when we contrasted global and local task performance solely under the local-saliency displays, we found left lateralization for global task performance and no lateralization for the local task performance. This lateralization still fits with the saliency-selection account we propose (as the global information was less salient under these conditions) but does not agree with a spatial-frequency specialization account. Nevertheless (and given the inconsistency of previous studies—as mentioned above), the failure to find lateralized responses to local and global targets should be treated cautiously.

Conclusion

Whereas TMS has been used to assess whether a region in the brain that was previously implicated in imaging or neuropsychological studies is functionally necessary for a task (Walsh & Cowey, 2000; Walsh & Rushworth, 1999), the present study represents one of the first instances in which fMRI is used following an initial finding using TMS in order to establish the exact brain area in which the function is being performed as well as to suggest the relevance of other functionally linked areas. Clearly, by feeding findings from one technique to the other, a better understanding of brain functionality can be achieved. For instance, following our results, further investigations can now target TMS at the specific brain structures identified in responding to low salient targets among high saliency distractors, in order to assess the time course of the suppression of saliency within the left IPS. Further investigations can also focus on a

potential functional division between different structures along the left IPS (e.g., the posterior and anterior segments of the left IPS) in this context. For now, however, the present findings strengthen the notion that there is lateralized functionality of the parietal cortex for selection based on saliency (Mevorach et al., 2006a, 2006b).

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Notes

1. As a result of a program error, behavioral data in the scanner were recorded only for 10 out of 12 participants.
2. This correlation still holds even when removing the outlier ($r = .59, p < .05$).
3. Note that for the global/local task the easy and hard conditions refer to target-salient and distractor-salient conditions, respectively.

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