Hierarchical visual processing is dependent on the oculomotor system

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Using functional MRI and eye movement recordings we studied the processing of hierarchical stimuli. In agreement with others, we found a minor left hemispheric dominance during local and right dominance during global processing. When attention was directed locally, well-known oculomotor cortical areas were activated, and saccades were elicited in 41% of the trials. Their latencies were similar to pro-saccades. During global processing virtually no saccades occurred. These results suggest two different operational modes of attention. Attending to local features induces a shift of attention, which simultaneously computes a saccade on any level above the brainstem with a computational burden equal to reflexive saccades. Conversely, attending to global features induces an expansion of the focus of attention, which reinforces fixation. *NeuroReport* 11:241–247 © 2000 Lippincott Williams & Wilkins.

Key words: Extrastriate visual cortex; Eye movements; fMRI; Frontal cortex; Human; Parietal cortex; Saccade; Sensorimotor processing; Superior colliculus; Visual attention

INTRODUCTION

Recognition and full appreciation of a natural scene require the visual brain to quickly extract characteristic features by integrating selected simple graphical attributes from its retinal image to form a suitable neural representation of important objects. This complex task is governed by attention, which, depending on the spatial scale, acts either like a lens zooming back and forth [1] or like a spotlight roaming about the visual surroundings, thereby enhancing and selecting global or local features, respectively. Furthermore, it is well known that shifting the spotlight may be accompanied by a saccadic eye movement (overt shift of attention) that quickly moves the fovea onto the area of interest or it may be achieved even as the eye maintains fixation (covert shift). Many investigations have addressed this close interaction between the operation of attention and oculomotor performance, and it is now generally believed that oculomotor processing is also active during covert shifts of attention [2]. Several imaging studies comparing overt and covert attention shifts have indicated that the oculomotor and attention systems can hardly be separated anatomically on the cortical level, as activation was found for both modalities in similar or equal occipital, parietal and frontal areas [3,4].

Hierarchical stimuli, such as letters composed of small letters [5] (Fig. 1), have been used extensively as a convenient probe for global and local feature processing. In most studies, which focused on the cortical level of computation, hemispheric specialization was evident for the control of spatial attention, such that the right hemi-

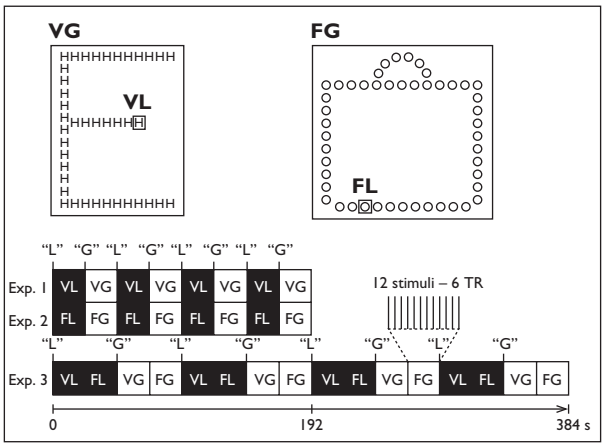

Fig. 1. Schematic view of the three fMRI experiments. VL, letter-based/attend local; VG, letter-based/attend global; FL, object-based/attend local; FG, object-based/attend global. TR = repetition time. Insets show examples of letter- (left) and object-based (right; suitcase made of circles) stimuli used in the experiments.

sphere mediated attention to global whereas the left hemisphere organized attention to local features [6–14].

The goal of this study was to address the effects of differential processing of hierarchical stimuli on cortical areas as well as oculomotor performance and to develop a preliminary neural model of attention-driven saccadic eye movements.

MATERIALS AND METHODS

fMRI experiments: Nine healthy right-handed male volunteers took part in the study. Imaging was performed on a GE 1.5 T Signa MRI scanner. Functional T2*-weighted images with a matrix size of 128×128 (voxel size $2 \times 2 \times 4$ mm) were obtained with an echoplanar single shot pulse sequence (EPI) using an axial slice orientation. Slices were acquired in an interleaved mode. Repetition time (TR) was 4 s, flip angle 50° and echo time (TE) 50 ms. The volume acquired covered the whole brain (30 slices of 4 mm). In the first two experiments a total of 54 and in the third a total of 102 whole brain images were acquired. In each sequence the first six images were discarded to assure equilibration of the MR signal. The scanning room was darkened during the whole experiment. The subject's head was fixed with Velcro straps and foam pads.

During scans subjects looked at a translucent screen via two mirrors. The viewing distance was 3m. The visual stimuli were back-projected onto the screen by an LCD video projector (480×640 pixels, 67 Hz refresh rate). Letter (A, E, F, H, I, K, M, N, V, W, X, Z) and object-based (anchor, arrow, circle, cup, ellipse, moon, rectangle, rhomboid, square, star, suitcase, triangle) hierarchical stimuli (Fig. 1) were centrally presented every 1.5 s for 300 ms. The stimuli were presented in black on a white background, subtending 14° horizontally and 11° vertically. The global and local form subtended 9° and 0.5°, respectively. All stimuli were non-congruent for the local and global level, and a specific letter was never consecutively presented on the local and global level. The spatial frequency of the stimuli (i.e., number of small items that made up the global form) was determined to make the object-based stimuli easily identifiable and was kept similar for the two stimulus classes. In fMRI experiment 1 and 2 a sequence of either letter- or object-based stimuli was presented. The order of the first two experiments was varied across subjects so that half of the subjects started with the letter-based and half with the object-based sequence. The subjects were instructed to attend to either the local or the global feature of the stimuli and internally name the appropriate letter/object. The local and global level was alternated every 24 s (12 stimuli). The change was indicated with a large red 'L' for the local and a large green 'G' for the global level that was presented at the beginning of the respective level. The two levels were repeated four times each adding up to a total of 192 s per experiment. Before subjects were positioned in the scanner a trial session was carried out to familiarize them with the task alternation and are a consistent naming of the objects. In experiment 3 the two stimulus classes were combined and the attention level was alternated every 48 s. The experiment always started with the local task, and the object-based stimuli always followed the letter-based stimuli before the attention level changed to global. The local and global sets consisted of 24 stimuli each and were repeated four times. The duration of experiment 3 was 384 s. See Fig. 1 for a schematic overview of all three experiments.

Image processing and statistical analysis were carried out using SPM99b [15]. All volumes were realigned to the first volume [16]. Head movements were < 2 mm for each subject. A mean image was computed on the basis of all realigned volumes. The mean image was spatially normalized into standard sterotactic space [17] using an EPI template. The data were smoothed using an 8mm (FWHM) isotropic Gaussian kernal. Data analysis was performed by modelling the conditions (two in experiments 1 and 2; four in experiment 3) as stimulus functions (box car function convolved with a hemodynamic response function) applying the general linear model. The calculated t-statistic was subsequently transformed into a Z-statistic. For the analysis of conditions $\times$ hemisphere effects a *t*-test for paired samples was applied on flipped *vs* unflipped subject-specific contrast image pairs ($p < 0.05$, uncorrected). Moreover, a preliminary analysis was performed to assess an interaction between conditions and eye movement performance, although eye movements and fMRI signals were sampled in two separate sessions. Regressions between the subject-specific contrast images ($p < 0.05$, uncorrected) and each subject's eye movement parameters were calculated.

Eye movement experiments: Unfortunately, there is no MR-compatible technique available yet to sample eye movements with the spatio-temporal resolution required for this study. Thus, eye movements had to be recorded in a separate session. Eye positions of the same nine subjects were measured using the magnetic search coil technique (SKALAR Medical, Delft, The Netherlands) [18,19]. Horizontal and vertical positions of the center-aligned right eye were sampled at 1000 Hz with a nominal spatial resolution of 30 s arc. We used an i486/50-based real-time computer system to control the experimental paradigm including stimulus presentation and data acquisition. The projection system was the same as in the fMRI experiment.

The same stimuli were used as in the fMRI experiment. Since eye positions could be sampled for each trial separately the stimuli were not presented in material specific (letter- and object-based) blocks. Within one experimental run the 24 stimuli were presented four times each in random order. The subjects were instructed to internally verbalize either the local or global aspect for each stimulus during a whole run. The stimulus presentation was automatically triggered after subjects successfully fixated a central fixation point during a period of 500 ms. Four runs (two local and two global) were presented. After these experiments, latencies of reflexive visually guided prosaccades were measured in all participants. Subjects were instructed to look from a central fixation point to an eccentric target that appeared randomly at 20°, 15°, 10°, and 5° to the right or left immediately (i.e. no gap or overlap) after a randomly chosen fixation period between 1000 ms and 500 ms. Each trial was followed by a 500 ms period of darkness. Twenty stimuli were presented for each of these eight conditions as well as a control (0° displacement), which yielded a total of 180 eye movement recordings.

All data processing was performed off-line using a

commercial software package (MATLAB 5.3, The MathWorks Inc., Natick, MA). Eye position was first filtered using an adaptive smoothing cubic spline and eye velocity was obtained by a two-point differentiation [20]. Finally, saccades were detected automatically using combined velocity and acceleration criteria. Two eye movement parameters were calculated for the correlation with the fMRI signal changes: the frequency of saccades was expressed simply as the ratio of the number of saccades executed and the total number of trials; the preferred direction of saccades was expressed as the ratio of the difference between rightward and leftward saccades and the sum of rightward and leftward saccades.

Since saccade latencies typically show a multimodal distribution (e.g. express saccades (~90–130 ms), fast regular (~140–170 ms) and slow regular (~190–230 ms) saccades), first-order statistical measures are not suitable to compare different sets of saccades. Therefore, a measure (R) was derived to illustrate that the range of the main mode of the visually guided reflexive and the locally directed saccades was similar. First, the range (t1–t2) of the main mode of the latency distribution obtained from visually (v) guided saccades was determined from its distribution by a combined peak and threshold method (defined as 10% of the maximum peak value). Second, R_v was computed as the ratio of the cumulative sum of latencies within this range (t1–t2) and the cumulative sum of all latencies. Lastly, R_l was derived applying the same range (t1–t2) to the latency distribution obtained from the locally directed attention task (l).

Statistical inference was obtained applying Wilcoxon's signed rank tests for paired samples.

RESULTS

fMRI experiments: Table 1 shows all significant changes in the MR signal for experiment 3. The main effects of attention level (globally *vs* locally directed attention) showed significant bilateral signal increase during local processing in the superior parietal lobule relative to global processing. The local maximum of this region, corresponding to Brodmann area (BA) 7 (see Fig. 2), was $x=-18$, $y=-78$, $z=52$ (Z-score 7.49) for the left, and $x=14$, $y=-76$, $z=56$ (Z-score 7.37) for the right hemisphere. Eight of the nine subjects showed significant activation in this region during the local task. Furthermore, significant bilateral activation was observed in the superior frontal gyrus (BA 6) and in the inferior occipital gyrus (BA 18). Globally directed attention yielded a bilateral increase in activation relative to local processing in the occipital cortex (BA 18, see Fig. 2). The activated area was larger and the peak of activation was more prominent on the right side. The local maximum on the right side was located at $x=14$, $y=-98$, $z=4$ (Z-score 7.35) and on the left side at $x=-6$, $y=-102$, $z=2$ (Z-score 5.97). The same regions were activated when the contrasts were computed for each modality separately (i.e. letter-based and object-based stimuli). Furthermore, the results of experiments 1 and 2 reproduced the results obtained in experiment 3 and did not yield additional information and are not explicitly listed in this report. All other possible contrasts including

Table 1. Significant fMRI signal changes in experiment 3.

Contrast	Brain area						Statistics		
	Anatomical	Functional	BA	Talairach			Z-score	p_v	p_c
				X	Y	Z			
L-G	l superior parietal lobule	PEF	7	−18	−78	52	7.49	<0.001	<0.001
	r superior parietal lobule	PEF	7	14	−76	56	7.37	<0.001	<0.001
	l superior frontal gyrus	FEF	6	−28	−4	64	5.15	0.010	0.005
	r superior frontal gyrus	FEF	6	32	4	66	5.33	0.004	0.005
	l inferior occipital gyrus	V2	18	−30[a]	−96	−6	5.51	0.002	<0.001
	r inferior occipital gyrus	V2	18	32[a]	−94	−12	5.23	0.006	0.005
G-L	r cuneus	V2	18	14[b]	−98	4	7.35	<0.001	<0.001
	l cuneus	V2	18	−6[b]	−102	2	5.97	<0.001	<0.001
VL-VG	l superior parietal lobule	PEF	7	−30	−58	48	6.65	<0.001	<0.001
	r superior parietal lobule	PEF	7	20	−70	56	5.76	<0.001	<0.001
	l superior frontal gyrus	FEF	6	−28	−6	64	5.68	0.001	<0.001
	r superior frontal gyrus	FEF	6	36	4	64	5.09	0.013	0.015
FL-FG	l superior parietal lobule	PEF	7	−10	−80	50	5.92	<0.001	<0.001
	r superior parietal lobule	PEF	7	14	−78	54	5.98	<0.001	<0.001
VG-VL	r cuneus	V2	18	18[b]	−98	4	5.59	0.001	<0.001
	l cuneus	V2	18	−6[b]	−100	2	5.62	0.001	0.002
FG-FL	r cuneus	V2	18	14[b]	−98	18	6.59	<0.001	<0.001

Coordinates (X, Y, Z) in Talairach stereotactic space refer to maximally activated foci associated with attention to global (G) and local (L) aspects of object-based (F) and letter-based (L) stimuli. The Brodmann area (BA) is given for each anatomical location. Only contrasts with significant activations are listed. *p* values were corrected for the entire volume either on the voxel level (p_v) or on the cluster level (p_c). Note the clearly different location of activation of V2 in the L-G contrast (a), which is much more peripheral compared to the peak activations of all G-L contrasts (b, G-L, VG-VL, and FG-FL) that broadly cover the representation of the fovea in V1 and V2. FEF, frontal eye field; PEF, parietal eye field; l, left; r, right.

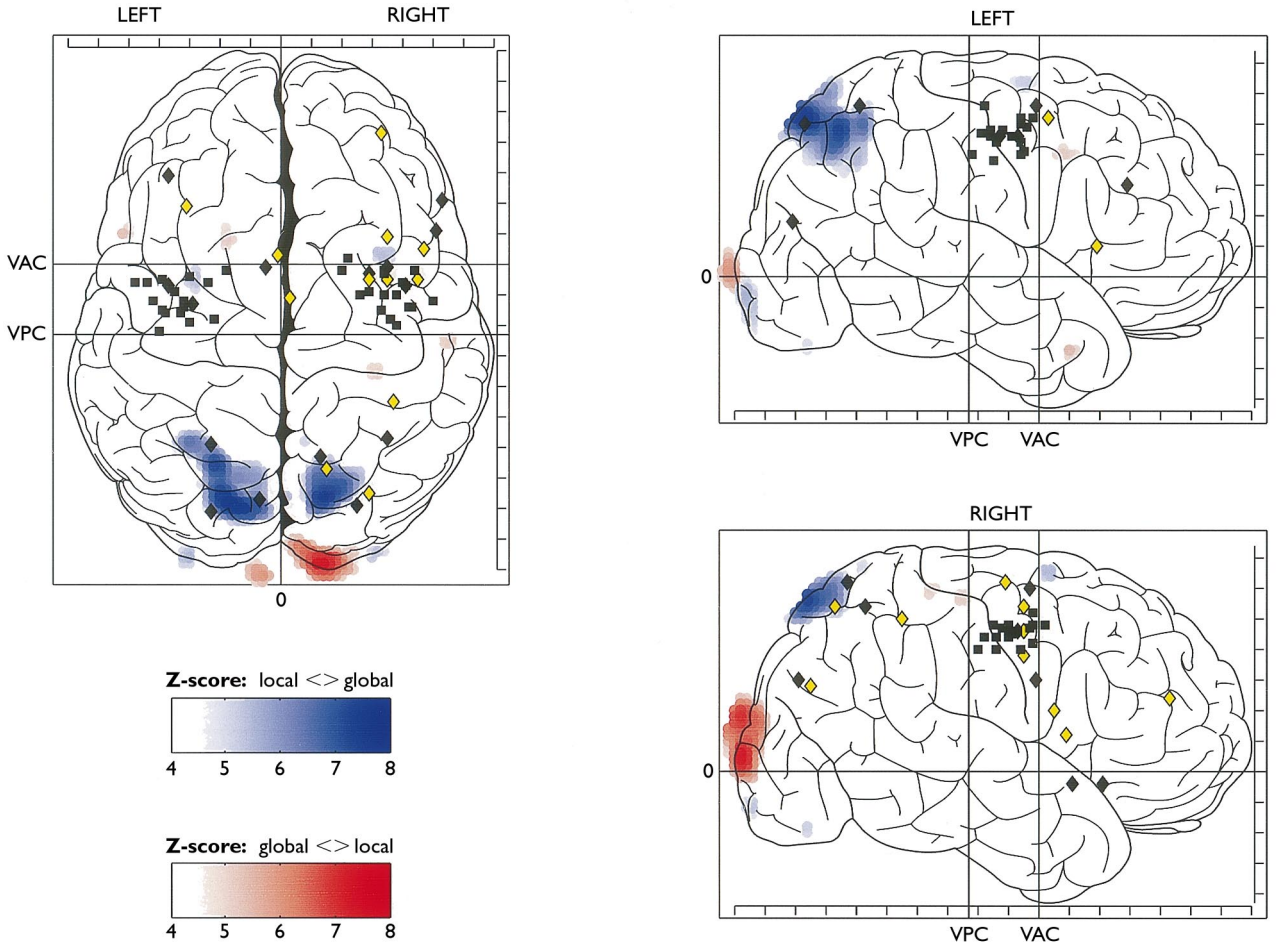

Fig. 2. Areas of significant activations ($p < 0.05$, corrected) shown as through-projections onto a representation of standard stereotactic space [17]. Blue: Locally directed attention (L-G). Red: Globally directed attention (G-L). Activation outside the representation of standard stereotactic space are due to residual inaccuracies of normalization but laid within the cortex in individual normalized brains. The peak activations of parietal and frontal eye fields as cited in [3] (diamonds) and [21] (squares) are overlaid. The color of the marker indicates whether the study consisted of an oculomotor task (black) or covert shift of attention (yellow).

the interaction between processing level (local *vs* global) and stimulus class (object-based *vs* letter-based) did not show any significantly activated areas. The hemispheric × condition effects were non-significant for all conditions ($p > 0.01$, uncorrected).

Eye movement experiments: Subjects executed significantly more saccades during the local (in $41 \pm 16\%$ of the trials) than during the global task ($3 \pm 2\%$; $p = 0.008$). Moreover, significantly more saccades were performed during local scanning of object-based stimuli ($48 \pm 19\%$) than of letter-based stimuli ($33 \pm 14\%$; $p = 0.008$). Except for subject S1 (in both directions), and for subjects S4 and S9 (in the non-preferred direction) the main modes of the latency distributions of reflexive visually guided (R_v) and locally directed (R_l) saccades were about equal ($R_{median} = 97$, $R_{mean} = 95 \pm 6$, range 77–100, $n = 14$; see Table 2). Furthermore, saccade direction during the local task did not differ significantly between letter-based (0.02 ± 0.55) and object-based (0.09 ± 0.66) stimuli.

Eye movement parameters and fMRI signal changes: Although the eye movements and the fMRI signal were not recorded simultaneously, a regression analysis was performed assuming intra-individual stability of the eye movement performance. In short, we found no interaction between any condition and eye movement performance.

DISCUSSION

A comparison with previous oculomotor and attention imaging studies [3,21] clearly shows that the areas activated in this study correspond to the parietal and frontal eye fields (see Fig. 2). During local processing subjects executed saccades in 41% of the trials but virtually none during global processing. Moreover, the latency of locally directed saccades did not differ from reflexive visually guided pro-saccades (see Table 2). This almost identical temporal characteristic strongly implies that the same neural process was employed for coding and triggering both sets of saccades (see Fig. 3). There is a remarkable variation across subjects both in the direction and fre-

Table 2. Saccade latencies.

Subject	Experiment	Leftward saccades							Rightward saccades						
		Statistics				Distribution			Statistics				Distribution		
		n	M	m	s.d.	t1	t2	R	n	M	m	s.d.	t1	t2	R
S1	v	79	174	176	26	135	220	94	81	177	179	27	135	245	96
	l	6	258	261	21			0	57[a]	247	243	32			53
S2	v	81	200	205	44	140	275	90	80	196	204	52	135	290	97
	l	45	197	189	38			90	73[a]	194	201	40			97
S3	v	79	218	220	46	135	325	97	80	210	222	53	140	305	94
	l	24[a]	265	255	28			100	13	227	218	44			100
S4	v	81	205	211	43	150	270	90	79	182	186	39	120	235	89
	l	71[a]	209	206	28			97	17	224	222	35			64
S5	v	78	207	218	38	170	260	90	82	201	206	38	150	285	95
	l	38[a]	209	214	30			88	20	241	232	46			91
S6	v	83	209	238	93	135	285	79	78	212	249	102	140	260	67
	l	30	199	201	29			100	61[a]	187	189	33			94
S7	v	79	210	231	59	150	335	96	82	225	240	69	145	395	95
	l	31	225	225	38			97	89[a]	206	214	31			100
S8	v	84	205	239	85	130	355	89	83	254	270	86	145	405	94
	l	132[a]	210	212	32			100	5	239	237	18			100
S9	v	82	183	187	29	145	230	95	81	182	191	42	140	230	86
	l	14	193	213	44			58	77[a]	204	208	33			77

Descriptive first order statistics are shown for leftward and rightward saccades for each subject ($n = 9$). *n*, number of saccades; [a]preferred direction; v, visually guided saccades; l, saccades elicited during locally directed attention task; M, median; m, mean. See text for explanation of R, t1 and t2.

quency of saccades. However, saccade direction was very constant for each subject. While we are aware that one of the major limitations of the present study is the fact that the fMRI signal and the oculomotor response were not sampled simultaneously, we nevertheless performed a preliminary regression analysis that revealed no covariation between the oculomotor response and the individual fMRI signal in the parietal and frontal cortex. The findings strongly support the hypothesis that shifts of attention and computation of eye movement parameters share a common pathway [3,4]. It remains to be shown whether there is intra-individual stability in the proportion of overt and covert execution of the local attention task. Subjects executed significantly more covert attention shifts when processing object-based than letter-based stimuli. However, there was no difference in activation of the parietal and frontal eye fields between these two stimulus categories.

Neural model: Altogether, these results suggest a simple neural model, which accounts for the oculomotor behavior during changes of the aperture of attention, as outlined in Fig. 3. There are two major modes: one will shift the focus of attention to a new spot of interest during local feature processing, and the other one will expand the focus during global processing. Shifting the focus is either overt and produces a saccade, or it is covert, in which case the saccade is computed but not executed.

Simplified synopsis of saccadic eye movements: Saccades are stereotyped eye movements that are spatially coded and triggered by a mutually inhibitory push-pull mechanism of pre-motor omnipause (OP) and burst-generator (BG) neurons, which are part of the brain stem oculomotor system (BOMS). Both OPs and BGs receive retinotopically organized input directly from the frontal eye fields (FEF) and the superior colliculi (SC). A complex neuronal network of the different layers of the SC itself is integrating direct retinal input (R) and various competing subcortical signals as well as cortical signals emerging from striate and extrastriate visual areas, e.g. V2 (BA 18), the parietal eye fields (PEFs), and mainly the FEFs with its direct as well as (caudally inhibitory) indirect pathway through the substantia nigra pars reticulata (SNpr). At this level, a similar push-pull interaction between the discharge activity (height of Gaussians) of rostral fixation neurons (FN) and more caudal buildup neurons (BUN), which are anatomically connected to the OPs and BGs respectively, decides whether and where a saccade should be made. During visual fixation FNs activate OPs, which prevent BGs from eliciting an unwanted saccade. After appearance of a novel visual target (e.g. T), retinotopically matching BUNs, which activate BGs, start firing while FNs and OPs are gradually inhibited [22]. Finally, if activity of a confined cluster of BUNs overrides the activity of the FNs, the BGs move the eyes to the spatial location coded by this particular cluster. However, while T conveys the movement signal to a possible new target, and therefore reflects and fully employs pre-motor computation of the metrics for an appropriate saccade, this process by itself does not guarantee to trigger an eye movement, since the neurons in the SC (FN and BUN) are functionally not tightly connected with their respective counterparts in the BOMS (OP and BG) [23]. Instead, this mechanism ensures that prior to each movement a target map is generated and an attention mechanism is engaged (covertly) that is necessary for the selection process by enhancing the response to relevant features. Hence, the SC acts as a complex sensorimotor engine processing command signals for the eye movement in

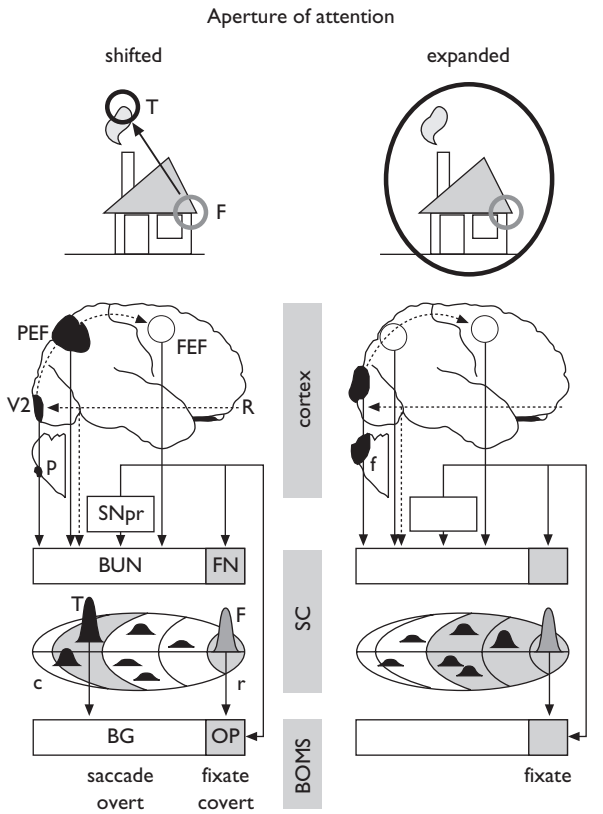

Fig. 3. Simplified schematic of a neural model of oculomotor behavior during different changes of the aperture of attention. There are two major modes, one will shift the focus of attention to a new spot of interest, and the other one will expand the focus. Shifting the focus is either overt and produces a saccade, or it is covert, in which case the saccade is computed but not executed and fixation is maintained. See text for details. Black areas in V2 and PEF represent original data (see Fig. 2). Heights of Gaussians indicate discharge activity of a cell cluster. T, novel visual target; F, point of fixation; PEF, parietal eye field; FEF, frontal eye field; R, retinal input; p, peripheral; f, foveal; SNpr, substantia nigra pars reticulata; BUN, buildup neuron; FN, fixation neuron; SC, superior colliculus (all layers merged); c, caudal; r, rostral; BOMS, brain stem oculomotor system; BG, burst-generator neuron; OP, omnipause neuron.

parallel with resolving conflicts in target selection occurring at various cortical levels by competitive inhibition. The occipital cortex contributes with feature maps extracted by pre-attentive segmentation, while the PEF reconstructs an observer-centered frame of reference from various spatial maps (visual, vestibular and somatosensory) and engages in the selection process by enhancing signals coding seemingly important objects. In addition, the FEF provides signals to the attention system that represent further weighting of relevant location vectors from the PEF in view of the behavioral context composed of a memory trace of previous motor outputs as well as expectancy and intention.

Shift of aperture of attention during local feature processing: At the outset, attention is allocated to the stimulus at the point of fixation (F, gray Gaussian). Upon appearance of a new scene, a pre-attentive map of likely stimulus locations (black Gaussians) is made available immediately to the attention system by R and the visual cortex. In this mode, locations distant from the fixation zone (F) seem to be preferred (caudal gray segment) as supported by the enhanced activity of V2 in peripheral retinotopic areas (see Table 1); and high activity of the PEF clearly indicates that this structure is computing a host of vectors to many possible targets in this area. The FEF, however, does not seem to carry a substantially higher computational burden compared to global processing and, therefore, shows little enhancement of activity (see Table 1). Subsequently, after stimulus locations are weighted, attention is allocated to the stimulus with the largest weight (T, the winner-take-all). However, whether a saccade will be triggered depends on the balance of activity between T and F, which itself is modulated concurrently by the FEF, and on additional modulation of the OPs by the FEF and other structures. According to our data, a saccade was executed in nearly 41% of the trials in this condition. Moreover, these eye movements essentially showed the same distribution of latencies as reflexive visually guided saccades (see Table 2) indicating that both sets share the same subcortical and cortical neural network.

Expansion of aperture of attention during global feature processing: The attention map (black Gaussians) progresses with a decaying gradient (gray area) from the fixation zone (F), thus functionally enlarging it. V2 (and most likely V1) now is active in a broad area around its foveal representation (see Table 1) in order to bind topographically distant features of the scene (e.g. the window and the smoke from the chimney). At the same time, activity in caudal regions of the SC is attenuated to prevent unwanted saccades, which might disrupt the demanding visual task. As a consequence, computational requirements for eye movements are minimal, and are reflected by the fact that the PEF is not active. During this condition, saccades were executed in only 3% of all trials, which strongly supports the hypothesis.

Hemispheric asymmetry: In agreement with previous studies [11–14], we found minor hemispheric asymmetries in cortical activation depending on the task.

Particularly, in the contrast of local versus global feature processing, the area comprising the left superior parietal lobule (PEF, BA 7) was slightly enlarged compared to the right hemisphere. Albeit only for the left side, PEF activity was also reported by Fink *et al*. [14]. However, unlike other studies [12–14], no asymmetry was found for V1 (BA 18) or for V2 (BA 19). These results are surprising in light of our assumption that local feature extraction is achieved by a shift of the aperture of attention, since it is generally agreed that the right parietal lobe is specialized for the control of spatial attention in the entire extrapersonal space. Indeed, a recent study by Gitelman *et al.* [24] clearly has demonstrated right hemispheric dominance in a task inducing covert shifts of attention to both sides. The reason for this apparent discrepancy is not yet fully understood, but could possibly be solved by changing the control condition used in this study (global feature extraction).

In the contrast of global *vs* local feature extraction, foveal representation of area V2 and possibly area V1 showed

enhanced activity on the right side. This result is substantially different from previous investigations, which report activation of the right areas V1 and V2 in their peripheral representation of the visual field [12–14]. This is possibly due to the fact that in these studies a much larger stimulus size was employed and, therefore, subjects at times produced a series of shifts of attention rather than expanding it for global apprehension.

There was no difference in activation between the letter- and object-based stimuli. The effects of stimulus category on the functional asymmetry described by others [13] may depend on the spatial frequency [14], which was kept similar across all categories in this study.

CONCLUSION

Bilateral regions in the occipital, parietal, and frontal cortex that correspond to well-known oculomotor areas are differentially activated during locally and globally directed attention to hierarchical stimuli. While processing local features, saccades are executed in about half of the trials indicating that the task can be executed either by overt or by covert shifts of attention. On the other hand, almost no saccades occur during processing of global features. These results strongly support the view that hierarchical processing is achieved by modulating the aperture of attention in at least two distinctly different ways. Due to the common pathway, each operational state automatically induces characteristic oculomotor reactions. It is not yet clear, however, which additional mechanism will finally cause neuronal activation within the brainstem oculomotor system, which is necessary to elicit the saccade that is already computed in cortical areas, such as the PEF and FEF, as well as the SC.

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