

Stefan Pollmann · Eran Zaidel · D. Yves von Cramon

The neural basis of the bilateral distribution advantage

Received: 26 August 2002 / Accepted: 1 June 2003 / Published online: 24 September 2003
© Springer-Verlag 2003

Abstract Letters can be matched by their physical identity (i.e., a–a: same/A–a: different) or by their name (both a–a and A–a: same). The latter, more demanding task has in previous experiments led to an advantage of bilateral over within-hemifield matches, which was not observed in the former. We have investigated the neural basis of this bilateral distribution advantage (BDA) in letter name matching with event-related fMRI. Unilateral, compared to bilateral, name matching led to increased activation in the contralateral fusiform and lateral occipital gyri. This increase went along with an ipsilateral increase of activation in homologous areas. Such a hemispheric resource sharing was not observed for letter shape matching. This pattern of activation shows that letter name matching induces hemispheric resource sharing in visual areas, which occurs when task demands in the hemisphere of input reach a critical level. Activation in anterior cingulate complex and posterior cingulate/retrosplenial cortex showed a task \times visual field interaction with lower activation for bilateral than unilateral name matches but higher activation for bilateral than unilateral shape matches, which fits the interhemispheric transfer demands in these tasks.

Keywords Bilateral distribution advantage · fMRI · Visual · Human

Introduction

Previous studies have presented evidence for a letter specific processing area in left lateral occipital cortex (Puce et al. 1996; Polk et al. 2000). These studies have compared the passive viewing of letters to the passive viewing of other stimuli, such as numbers, faces or textures. However, identification of a letter is not tied to a specific physical form. For instance, both A and a denote the same letter, although they differ in their physical shape. In the current study, we used event-related functional magnetic resonance imaging (fMRI) to analyze the neural structures which are involved in letter name identification, in comparison to letter shape identification. We used the paradigm of letter name and letter shape matching, which is based on a classic experiment by Posner (1969). He asked participants to decide as quickly as possible whether two letters were the same. He found that when two letters were presented simultaneously, participants detected the identity match (e.g., A-A) much faster than the name match (A-a). Only when the two letters were presented successively with a stimulus-onset asynchrony (SOA) of 1 s or longer were identity and name matches equally fast. This indicates that letters are initially held in a visual format that represents their shape, before they become transformed into an abstract code.

In subsequent experiments using a variant of this paradigm, it was observed that letter name matching is faster when the two letters to be matched are presented simultaneously one in each visual hemifield, compared to presentation within one hemifield (Banich and Belger 1990; Belger and Banich 1992; Banich 1998). Such a bilateral distribution advantage (BDA) was usually not observed for letter shape matching. The explanation offered for this dissociation was that from a certain level of task complexity, it may be advantageous to distribute processing over both cerebral hemispheres in order to use their joint resources. In this case, bilateral matching is advantageous, because the stimulus input is initially distributed over both hemispheres, which reduces the amount of callosal transfer. On the other hand, for simple

S. Pollmann (✉) · D. Y. von Cramon
University of Leipzig, Day Clinic of Cognitive Neurology,
Liebigstr. 22a,
04103 Leipzig, Germany
e-mail: pols@medizin.uni-leipzig.de
Tel.: +49-341-9724284
Fax: +49-341-9724269

S. Pollmann · D. Y. von Cramon
Max-Planck Institute of Cognitive Neuroscience,
Leipzig, Germany

E. Zaidel
Department of Psychology, University of California,
Los Angeles, California, USA

tasks, which can easily be processed within the hemisphere which receives the stimulus input, within-hemifield presentation is optimal, because all necessary information is received by one hemisphere which does the processing, thus eliminating the need for callosal transfer of stimulus characteristics. This leads to the interesting prediction that the amount of interhemispheric transfer is high for unilateral name and bilateral shape matches, whereas it is low for bilateral name and unilateral shape matches.

In contrast to previous experiments, which measured response times, the use of fMRI allows a more specific investigation of the processing step (or steps) at which interhemispheric resource sharing occurs. Thus, in the present study, we were interested to see whether (and where in the brain) we could find evidence for bilateral processing in letter name, but not letter shape, matching. We were further interested in the brain areas which may be involved in callosal transfer. Such areas should show an interaction of presentation (uni- versus bilateral) \times task (name versus shape match).

In the current experiment, we presented four letters simultaneously, two in each visual hemifield (Fig. 1). The locations of two letters were cued just prior to letter presentation, to indicate which of the letters were to be matched. In one-half of the experiment, subjects were instructed to match letters by physical shape, whereas in the other half they had to match letter name. Of course, letter name matching should involve additional lexical processing stages beyond the perceptual stages necessary for letter shape matching. However, complete commissurotomy patients can match letters by shape and by name, as long as they are presented within the left or right visual hemifield (Eviatar and Zaidel 1994). This shows that letter name matching does not critically depend on high-level linguistic processes lateralized to the left hemisphere. Thus, we were especially interested in the early stages of visual letter identification. Specifically, we expected activation in left lateral inferior occipital and fusiform gyri, which were more strongly activated in previous studies when subjects passively viewed letter strings than when they viewed other items, such as faces and textures (Puce et al. 1996) or digits (Polk et al. 2000).

Materials and methods

Subjects

Fourteen subjects took part in the experiment. Informed consent was obtained from all subjects according to the guidelines of the Max-Planck Institute. The experiment was approved by the ethics review board of the University of Leipzig. The data of three subjects were discarded because of high error rates (14%, 15%, and 31%; cutoff criterion was >10% errors), which rendered interpretation of their reaction time data questionable. The remaining 11 subjects made an average of 6% (SD=2.39%) errors. Subjects age ranged from 18 to 25 years. Eight subjects were female. All were right-handed, assessed with the Edinburgh Handedness Inventory (Oldfield 1971).

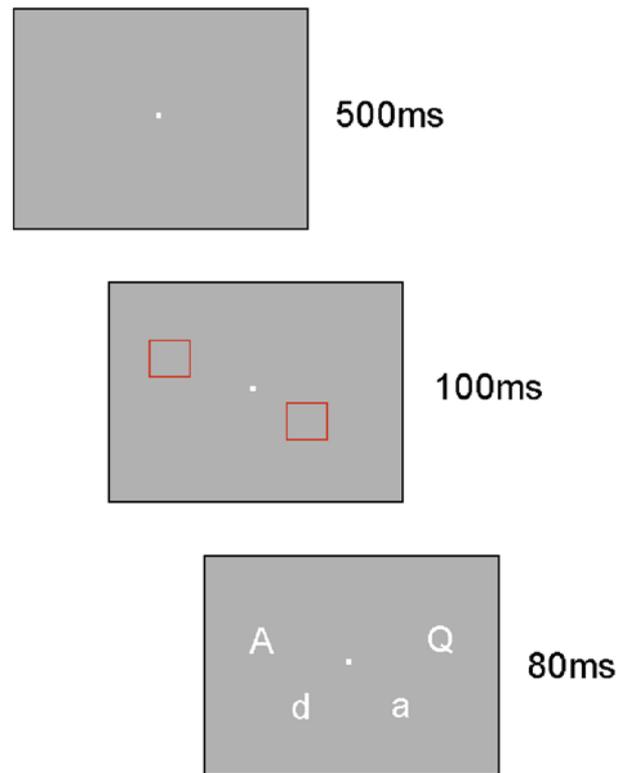


Fig. 1 Trial description. After a fixation period, two rectangular red boxes were flashed to cue the positions of the two letters, out of four presented immediately afterwards, which had to be matched. In separate blocks, either physical shape or letter name had to be matched

Experimental design

In the present study, we used a new experimental design, which eliminated hemispheric perceptual load differences and reduced left-to-right scanning patterns which may have contaminated previous data. Prior versions of this task presented perceptually unbalanced displays. A common version compares matching two letters within the same VF with matching two letters, one in each VF. Unfortunately, in this design within and between trials have different perceptual loads, as do the perceptual loads of the two hemispheres in within matches. A more recent version compares a bottom letter in one VF with two top letters, one in each VF (e.g., Banich and Belger 1990). This design equates the perceptual load in the within and between conditions but it does not equate the perceptual load of a stimulus display on the two hemispheres. Furthermore, this design may engage a left-to-right scanning pattern of the two top letters. Instead, we used a design with four letters in each stimulus display: two on the bottom in each VF and two on the top in each VF (Fig. 1). The two target letters to be compared are cued peripherally by a frame. This design equates the perceptual load across the within and between conditions, as well as across the two hemispheres. It avoids the scanning pattern and reduces but does not eliminate the BDA, compared to the three-stimulus design (Copeland 1995; Copeland and Zaidel 1996).

Trials began with presentation of a central fixation point for 500 ms, which was followed by presentation of two red rectangular frames of 0.9° side length, which cued the letters to be compared. The cues persisted for 100 ms and were immediately followed by presentation of four letters, which appeared simultaneously at the four positions of the display for a duration of 80 ms. A blank screen was presented for 1920 ms until presentation of the next trial. We presented upper- and lowercase Helvetica fonts of the letters A, B, D, E, G, H, N, Q, and R. Uppercase letters were 0.5° high and 0.4°

wide, lowercase letters $0.4^\circ \times 0.3^\circ$. Of the four letters, two were presented 1.4° above fixation and 2.4° to the left and right of the midline and the remaining two letters 1.4° below and 1.4° to the left and right of the midline. Thus, the display was asymmetrical, with the upper field letters presented more lateral than the lower field letters. This arrangement was chosen to equate the scanning of the cued positions in the within and cross-hemifield trials as far as possible and to minimize a potential advantage of between hemifield matches due to the fact that scanning from left to right might be faster than from top to bottom. The same stimuli were used for shape and name matching.

The experiment consisted of 20 blocks of 36 trials each. In one-half of subjects, the first ten blocks represented the name condition and the second ten blocks the shape condition. In the other half of subjects this order was reversed. The first two blocks of the name and shape condition, respectively, served as training and the data were discarded. In one-third of the trials, the two letter positions in the left visual hemifield (LVF) were cued, in another third the positions in the right visual hemifield (RVF) were cued and in the remaining third bilateral positions (BVF) were cued. Bilateral cues were either presented in the left upper and right lower position, or in the left lower and right upper position. The letters at the cued positions were matches in 50% of the trials of each condition. The sequence of cue positions, letters, and matches/non-matches was individually randomized. Name matches did not match in physical letter shape. Half of the subjects began responding with their right or left hand. Response hand was changed every two blocks. The fMRI experiment consisted of two scans of ten blocks each. Fixation periods of 30 s duration were inserted at the beginning and end of each scan, and between blocks. On the day before the fMRI experiment, subjects took part in a training session consisting of the same experiment which was run in the scanner.

fMRI procedures

The fMRI data were acquired at a field strength of 3 T (Medspec 30/100, Bruker, Ettlingen) using a gradient-recalled EPI sequence with a TR=2000 ms, TE=30 ms, and a flip angle of 90 degrees. The matrix size was 64×64 , FOV 19.2 cm, with 100 kHz sampling. Sixteen axial slices were acquired with 5 mm slice thickness and 2 mm interslice gap. The slices were oriented horizontally with the 5th most inferior slice in the AC-PC plane. The data were analyzed with the software package LIPSIA (Leipzig Image Processing and Statistical Inference Algorithms; Lohmann et al. 2001). First, slice acquisition time differences were corrected by sinc interpolation. Then, data were corrected for movement artifacts (Friston et al. 1996). In the spatial domain, the data were filtered with a Gaussian filter with FWHM=12 mm. Following this preprocessing, the functional datasets were coregistered with the subjects individual high resolution anatomical datasets and normalized by linear scaling. Data were analyzed using the general linear model (Friston et al. 1995). Low frequency drifts were removed by high-pass filtering with a cutoff frequency of 1/30 Hz. Event-related analyses were computed using a model of the hemodynamic response and its temporal derivative (Josephs and Henson 1999). The significance criterion was $\alpha=0.0001$ (uncorrected) for whole brain analyses and $\alpha=0.0005$ for analyses restricted to occipital cortex. Group activation was calculated by one-sample *t*-tests at corresponding voxels of the individual SPM $\{z\}$ across subjects (Bosch 2000). We have previously shown that rapid event-related designs such as the one used here allow the measurement of the differential response between experimental conditions without amplitude loss due to BOLD overlap of successive trials (Pollmann et al. 2000a; for a model approach cf. Friston et al. 1999). For the analysis of amplitude changes in regions of interest (ROI), we extracted the signal time course at the voxel with the highest activation within the activated ROI. We then calculated the maximal signal change, compared to the voxel mean across the experiment, which occurred in a time window between 4 s and 8 s after stimulus onset. *t*-Tests

for paired samples were run to test the stimulus-load and selective bilateral processing hypotheses. Significance criterion was $\alpha=0.05$.

Results

Behavioral data

We calculated a repeated measures ANOVA with the factors task (name vs. shape match), visual hemifield (BVF, LVF, RVF) and response (match, non-match). This analysis yielded significant main effects for task ($F_{(1,10)}=40.10$; $p<0.05$), and response ($F_{(1,10)}=69.37$; $p<0.05$) and a marginally significant main effect for VF ($F_{(1,10)}=3.45$; $p=0.052$). Significant interactions were observed between task \times response ($F_{(1,10)}=26.63$; $p<0.05$) and VF \times response ($F_{(2,20)}=5.32$; $p<0.05$). Name matches were generally slower than shape matches and non-matches of both kinds were slower than matches. The expected interaction for task \times VF, which would be expected for a name-match-specific BDA, was not observed in this overall analysis. Instead both task and VF interacted with response.

We further analyzed the influence of the response by calculating separate ANOVAs on the factors task and hemifield for correct target present and target absent responses. The ANOVA on target present responses yielded significant main effects for task ($F_{(1,10)}=25.73$; $p<0.05$) and VF ($F_{(2,20)}=7.44$; $p<0.05$). There was a trend towards an interaction between both factors ($F_{(2,20)}=2.63$; $p=0.097$). The corresponding analysis on target absent responses yielded only a significant main effect of task ($F_{(1,10)}=52.27$; $p<0.05$).

Inspection of the response times (Fig. 2) suggested that the nonsignificant task \times VF interaction was due to the presence of a name-match specific BDA in the comparison of BVF and RVF matches, but not in the comparison of BVF and LVF matches. This impression was supported by separate ANOVAs for task (name, shape matches) and VF (BVF, LVF) or VF (BVF, RVF). In the analysis of bilateral and LVF matches, we found significant main effects for task ($F_{(1,10)}=18.24$; $p<0.05$) and VF ($F_{(1,10)}=52.27$; $p<0.05$), whereas the interaction was not significant. In the analysis of bilateral and RVF matches, we found a significant main effect of task ($F_{(1,10)}=19.16$; $p<0.05$), a trend in the main effect of VF ($F_{(1,10)}=3.67$; $p=0.084$) and a significant interaction ($F_{(1,10)}=5.04$; $p<0.05$).

Figure 2 shows the nature of this interaction: Bilateral name matches were significantly faster than within-RVF name matches ($t_{(10)}=3.23$, $p<0.05$), whereas there was no significant difference between bilateral and within-RVF shape matches ($t_{(10)}=0.26$; $p>0.05$). In contrast, letter name ($t_{(10)}=2.84$; $p<0.05$) and letter shape matches ($t_{(10)}=2.27$; $p<0.05$) in the LVF were both significantly slower than bilateral matches. Thus, we found the expected name-match selective bilateral distribution advantage in the comparison of bilateral versus RVF matches, whereas compared to LVF matches bilateral presentation was advantageous both for name and shape matching.

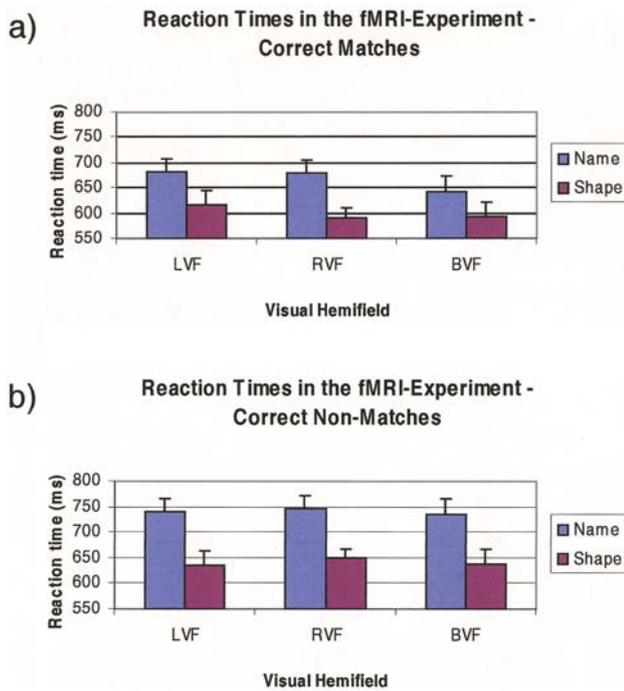


Fig. 2a, b Reaction times obtained during the fMRI experiment. **a** Correct match responses; **b** correct non-match responses (*Name* letter name comparison, *Shape* letter shape comparison, *LVF* left visual hemifield, *RVF* right visual hemifield). *Error bars* represent standard errors of means

Functional imaging

Because the bilateral distribution advantage is of central interest, we start with an analysis of contralateral load effects and associated spread of activation to homologous ipsilateral brain areas. Next we analyze the task \times VF interaction, which may yield brain areas involved in interhemispheric transfer in letter name and shape matching. This is followed by the analysis of the task and VF main effects. We consider only trials with correct matches, because the reaction time analysis demonstrated that the BDA effect was not present in the target absent responses.

Load effect and hemispheric resource sharing

It was proposed that the BDA for name matching is a consequence of bilateral processing that occurs even for unilateral name matches. This utilization of bihemispheric resources is thought to result from resource limits in the hemisphere of input due to the higher task demands of name matching, in contrast to shape matching. We were thus looking for brain areas which showed higher activation for contralateral within-field name matches than for bilateral name matches. This was expected as a sign for increasing work load in the hemisphere of input. At the same time we looked for ipsilateral activation during unilateral name matches in homologous areas to those showing a load effect. This was expected as an indicator for hemispheric resource sharing as a conse-

quence of work load reaching some critical level in the hemisphere of input. Both the load effect and the resource sharing in homologous areas were not expected to occur in the simpler shape matching task.

The pattern of contralateral load effect and spread of activation to homologous ipsilateral areas was only found in ventral occipital cortex. Name matches elicited significant differential visual cortex activations of a different kind: Unilateral matches led to higher activation in the hemisphere of input than bilateral matches, indicating that processing of two letters posed significantly higher demands than processing of a single letter within the contralateral hemifield. Contrasting bilateral with LVF matches, this activation pattern was found in posterior and anterior fusiform locations (Fig. 3a, c). Contrasting bilateral with RVF matches, it was found in the left lateral occipital gyrus, extending into posterior fusiform gyrus (Fig. 3d). In contrast, unilateral shape matches did not lead to higher activation in the hemisphere of input than bilateral matches (Fig. 3a, c), supporting the view that for shape matches processing of two versus one contralateral letters did not pose increased demands on visual areas.

When we compared activation induced by bilateral shape matches minus activation by shape matches within the LVF, we found increased activation in left lateral occipital gyrus, i.e., in the hemisphere which received contralateral task-relevant input only with bilateral presentation (Fig. 3a). Likewise, comparing bilateral minus within-RVF shape matches yielded a significant, but smaller activation in right posterior fusiform gyrus, bordering the collateral sulcus (Fig. 3c). Comparable activations were not observed for name matches: bilateral name matches–LVF name matches did not lead to increased activation in left visual areas and bilateral name matches–RVF name matches did not lead to increased activation in right visual areas (Fig. 3b, d). This suggests that during unilateral name matches, the ipsilateral hemisphere was involved in letter processing. This is further illustrated by the signal change obtained in the activated areas. Especially in left lateral occipital and fusiform gyri (Fig. 3a, d), ipsilateral (LVF) name matches elicited as much activation as bilateral matches, whereas ipsilateral shape matches elicited almost no activation. In right fusiform gyrus (Fig. 3c), these differences were less pronounced.

Interaction of task and visual hemifield

The interaction between hemifield (BVF, RVF) and type of match (name, shape), which determined the name-selective BDA in the reaction time data, was also calculated for the functional images. (The interaction was defined by the formula: (name_BVF–name_RVF)–(shape_BVF–shape_RVF)). Significant changes of the BOLD response were observed in the anterior cingulate complex (ACC complex; BA24/32) as well as the posterior cingulate/retrosplenial cortex (Fig. 4). In addition, the left postcentral gyrus was activated.

Type of Match: Shape Name

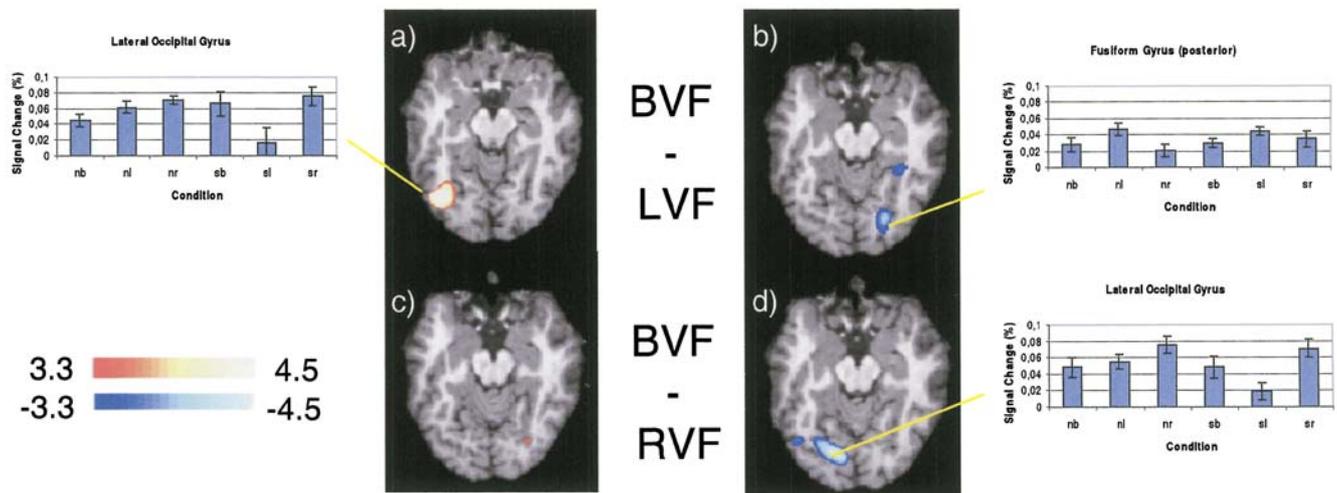


Fig. 3a–d Contralateral load effect and spread to ipsilateral ventral occipital cortex in name matching but not shape matching. The functional images represent ventral occipital activation foci obtained in the contrasts of BVF–LVF (*upper*) and BVF–RVF (*lower*) matches. The *left row* represents shape matches, the *right row* name matches. Left hemisphere is *on the left*. Color scales indicate positive and negative z -values. Positive z -values represent higher activation for bilateral, negative values higher activation for unilateral matches. **a** BVF shape matches elicited a significant signal increase over LVF shape matches in left lateral occipital cortex at $x=-41, y=-76, z=0$ (in coordinates of Talairach and Tournoux 1988) and **c** a weaker increase compared to RVF matches in right posterior fusiform gyrus ($x=22, y=-77, z=1$). No significant negative z -values were observed in the areas shown. Signal changes elicited by name matches. **b** The negative z -values indicate higher

activation for LVF matches compared to bilateral matches in the right anterior ($x=28, y=-45, z=-8$) and posterior ($x=16, y=-79, z=1$) fusiform gyrus. **d** Significantly higher signal strength for RVF matches compared to bilateral matches was observed in the left lateral occipital gyrus ($x=-44, y=-71, z=-3$) and fusiform gyrus ($x=-17, y=-83, z=0$). No significant positive z -values were observed in these contrasts. *Graphs* indicate peak signal amplitude per condition and ROI (nb name comparison, bilateral, nl name comparison, LVF, nr name comparison, RVF, sb shape comparison, bilateral, sl shape comparison, LVF, sr shape comparison, RVF). *Error bars* indicate standard error of mean for within subject designs (Loftus and Masson 1994). For overlapping activation foci (left lateral occipital gyrus in **a** and **d** and right posterior fusiform gyrus in **b** and **c**, only a single signal amplitude graph is provided

The negative z -values in these areas indicate less activation for bilateral–RVF name matches relative to bilateral–RVF shape matches. In order to analyze the exact nature of this interaction, we extracted the signal amplitudes in the anterior and posterior cingulate activations. In the ACC complex, activation was significantly higher for bilateral shape matches than for bilateral name matches ($t_{(10)}=4.08, p=0.002$), whereas there were no significant differences between name and shape matches in the RVF or in the LVF (both $t_{(10)}<1.18; p>0.05$). Thus, the anterior cingulate cortex was differentially involved in bilateral matches of name and shape. The pattern was similar in the posterior cingulate cortex. Bilateral shape matches elicited higher activation than bilateral name matches ($t_{(10)}=2.11; p=0.061$), whereas there were no significant differences between name and shape matching in the LVF or RVF (both $t_{(10)}<0.11; p>0.916$).

Comparison of letter name and shape matching across positions

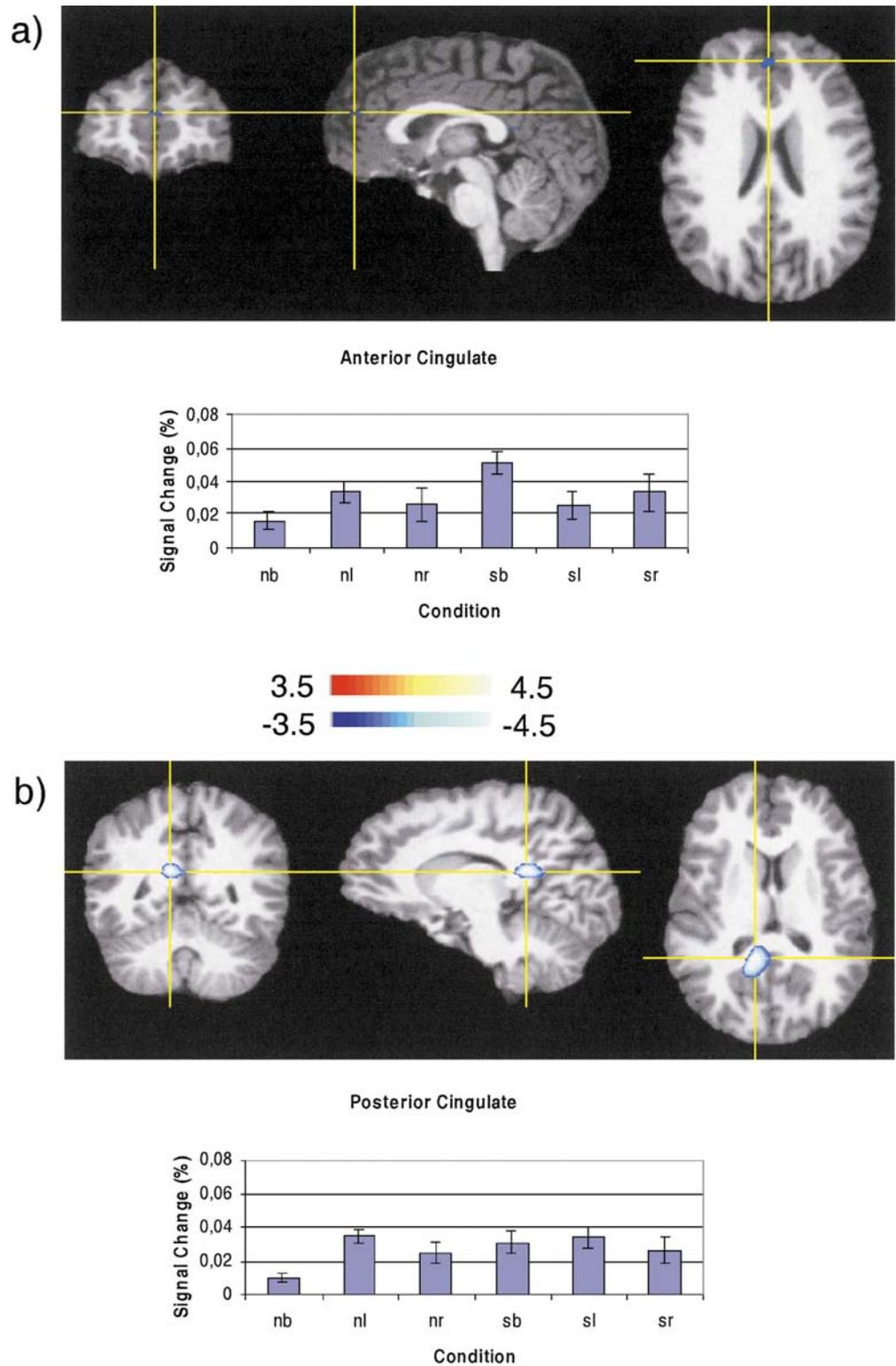
Another possible source of the BDA effect may be that successive processing stages are distributed over the

hemispheres to increase efficiency (Belger and Banich 1998). This variant of computational complexity would predict that additional brain areas, subserving additional processing steps, are activated by name matching compared to shape matching.

Increased activation for letter name matching

We calculated the contrast between correct positive letter name and letter shape matches to find the areas which showed stronger activation for letter name matches. Significant activations were found left lateralized in posterior brain areas and bilaterally in frontal cortex (Table 1). Specifically, a strong activation was found in left posterior inferior occipital cortex, bordering temporal cortex (Fig. 5a). Moreover, a chain of activation foci followed the left intraparietal sulcus, one focus located in the descending segment, in the vicinity of the junction with the transverse occipital sulcus, another located along the horizontal segment, and a third located in the ascending segment, near the junction with the postcentral sulcus. A small activation was found in the right middle temporal gyrus.

Fig. 4a, b Functional interaction of task and hemifield. Interaction of type of match (name, shape) \times visual hemifield of matched letters (bilateral, RVF). The peak activations were observed at **a** $x=-2, y=48, z=8$ in the ACC complex and **b** at $x=-11, y=-44, z=19$ in posterior cingulate/retrosplenial cortex. Left hemisphere is *on the left*. Graphs show peak signal amplitude per condition and ROI. Abbreviations are the same as in Fig. 3



In frontal cortex, activations were observed bilaterally at the junction of the inferior precentral and inferior frontal sulci. Further activations were found bilaterally in the anterior parts of the superior and middle frontal gyri, including a large activation in right frontopolar cortex.

Activations were also found bilaterally in the anterior insula.

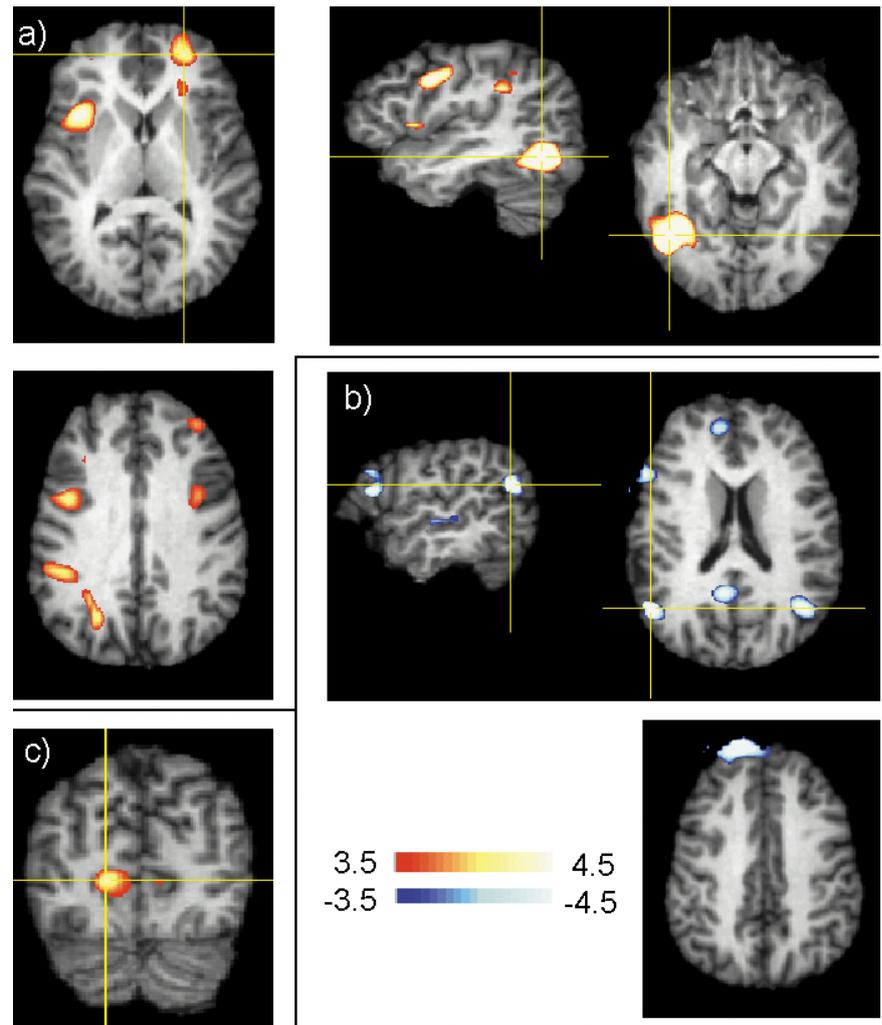
Increased activation for letter shape matching

The reverse contrast, letter shape–letter name matches, yielded significant activations in a bilateral frontoposterior network (Table 1). Major foci of activation were seen in the posterior parts of the superior temporal gyri bilaterally (Fig. 5b). A chain of activations was further observed

Table 1 List of functional activations (Z_{max} maximum Z-score, *Hemi* hemisphere, *x*, *y*, *z*-coordinates according to Talairach and Tournoux 1988)

Contrast	Z_{max}	Hemi	<i>x</i>	<i>y</i>	<i>z</i>	Structure
Name matching > shape matching	4.26	R	32	49	14	Superior frontal gyrus
	4.65	R	22	48	-5	Superior frontal gyrus
	3.94	R	29	36	23	Middle frontal gyrus
	4.65	L	-34	25	17	Inferior frontal gyrus
	3.89	R	47	20	-5	Inferior frontal gyrus
	4.39	R	31	13	19	Inferior frontal gyrus
	5.63	L	-34	4	30	Precentral gyrus
	3.79	R	22	30	-2	Anterior insula
	5.18	L	-37	15	1	Anterior insula
	3.6	L	-4	13	42	Frontomedian wall (preSMA)
	3.88	L	-2	11	23	Anterior cingulate
	4.27	R	46	-21	-11	Middle temporal gyrus
	4.02	R	31	-25	-13	Hippocampus
	4.59	L	-43	-33	32	Inferior parietal lobule
	5.62	L	-26	-49	44	Superior parietal lobule
	Shape matching > name matching	7.64	L	-44	-67	2
-3.8		L	-25	63	-6	Superior frontal gyrus
-6.1		L	-25	46	38	Superior frontal gyrus
-5.3		R	19	38	46	Superior frontal gyrus
-3.9		R	7	28	54	Superior frontal gyrus
-5.3		L	-55	23	8	Inferior frontal gyrus
-3.8		R	58	-6	29	Precentral gyrus
-4.2		L	-43	-15	57	Precentral gyrus
-3.8		R	40	-18	55	Precentral gyrus
-4.8		R	23	-29	60	Postcentral gyrus
-4.3		L	-47	20	-31	Superior temporal gyrus
-4.5		L	-56	-19	0	Superior temporal gyrus
-4.7		R	58	2	-16	Middle temporal gyrus
-3.9		L	-58	-1	-30	Middle temporal gyrus
-3.9		L	-62	-12	-13	Middle temporal gyrus
-4		R	46	-9	4	Posterior insula
-5.2		L	-28	-26	-4	Hippocampus
-4.2		L	-1	-43	14	Posterior cingulate
-6		L	-11	-45	32	Inferior precuneus
-4.9		L	-64	-58	17	Superior temporal gyrus, posterior segment
-5.7		L	-52	-58	29	Superior temporal gyrus, posterior segment
-5.2		R	47	-59	26	Superior temporal gyrus, posterior segment
-4		L	-2	-95	16	Cuneus
-4		L	-29	-89	-11	Inferior occipital gyrus
-4.1		R	25	-39	-22	Fusiform gyrus
-4.9		R	13	-23	-5	Substantia nigra
-5.8	L	-32	-86	-23	Cerebellum	
Bilateral > unilateral matching	3.72	R	28	9	29	Middle frontal gyrus
	3.72	L	-14	7	29	Cingulate gyrus
	4.66	L	-16	-77	12	Area striata
	3.56	R	7	-77	12	Area striata
Unilateral > bilateral matching	-3.7	L	-64	-25	-1	Middle temporal gyrus
Interaction: type of match \times VF ($name_{bi}-name_r$)-(shape $_{bi}$ -shape $_r$)	-4.36	L	-40	-18	29	Postcentral gyrus
	-3.63	L	-2	48	9	Anterior cingulate gyrus
	-4.75	L	-11	-45	20	Posterior cingulate gyrus/retrosplenial cortex

Fig. 5a–c Functional activation elicited by name versus shape matching across visual hemifields and by bilateral versus unilateral matches across tasks. *Upper section and lower right section* Letter name minus shape matching. The upper section (**a**) shows brain areas with higher activation following name matches, whereas the lower right section (**b**) shows areas with higher activation for shape matches (indicated by negative Z-scores). *Lower left image (c)* Bilateral versus unilateral matching across tasks. Left hemisphere is *on the left*. Color scales indicate positive and negative z-values



along the superior frontal gyri of both hemispheres, reaching into the middle frontal gyri. Approaching the frontal pole, the activation was left-lateralized, ending in an activation in left frontopolar cortex.

Activations were further observed in the anterior frontomedian wall and the posterior cingulate and retrosplenial cortices and bilaterally in the cerebellum.

Thus, the additional areas activated in the name matching task, compared to shape matching, may support the computational complexity account. However, the additional areas of activation observed for shape matching compared to name matching show that a simple additive factors logic cannot account for the differences between both tasks.

Comparison of bilateral versus unilateral matches across tasks

Finally, we were interested to see which brain areas were, across tasks, more activated by bilateral matches compared to unilateral matches. It has been proposed that the right hemisphere may be better suited to attentively process stimuli from both hemifields, whereas the left hemisphere

would attend mainly to contralateral stimuli (Heilman and Valenstein 1979; Mesulam 1981).

Significantly stronger activation for bilateral versus unilateral matches, across tasks, was observed in striate cortex, in keeping with the retinotopic organization of this cortex. Interestingly, the activation was much stronger in the left hemisphere, compared to the right (Fig. 5c).

A small activation was observed at the horizontal segment of the right intraparietal sulcus. Further activations were observed in left anterior middle frontal gyrus and right posterior middle frontal gyrus and in left anterior cingulate cortex (BA33).

The reverse, stronger activation for unilateral compared to bilateral matches was observed in the middle part of the left middle temporal gyrus, bordering superior temporal sulcus.

Discussion

Neural basis of the bilateral distribution advantage

We used fMRI to investigate the hypothesis that the selective BDA for letter name matching is based on

hemispheric resource sharing in letter name matching, which does not occur in letter shape matching. We further wanted to know whether this resource sharing occurred at a particular processing stage.

We found that the BDA for letter name matching went along with increased activation for name over shape matching in lateral occipital and fusiform gyri in the hemisphere contralateral to stimulation. These contralateral signal increases, in turn, went along with spread of activation to homologous areas of the ipsilateral hemisphere. The lateral occipital and fusiform gyri are well known to support visual object recognition and, in the case of left lateral occipital cortex, have been demonstrated to be specifically sensitive to visual letter processing (Puce et al. 1996; Polk et al. 2000).

It should be noted that, in every trial, two letters were presented in each hemifield (Fig. 1), so that these activation differences were not due to differences in physical stimulation, but to attending the cued locations within or across hemifields. A potential confound may be that the location of the cues necessarily differed between bilateral and unilateral matches. However, these asymmetries cannot explain the visual-hemifield-dependent differences between name and shape matching, which are of central interest in this paper.

The pattern of activation observed in the visual areas was not observed outside of occipital cortex. Thus, only occipital areas showed both increased contralateral activation and homologous ipsilateral activation in name matching. We conclude that visual letter processing is the most likely step at which a resource limit in the hemisphere of input leads to bilateral resource sharing in letter name matching. Thus, the BDA for letter name matching may be explained by the fact that name matching poses higher demands on visual letter processing than letter shape matching, and that this increased demand leads to the recruitment of functionally homologous ipsilateral cortex. This hemispheric resource sharing, in turn, may lead to the BDA.

The BDA observed in previous behavioral studies has been explained with the notion that hemispheric resource sharing may be advantageous in tasks with higher computational complexity (Belger and Banich 1992, 1998; Weissman and Banich 2000). These studies showed that both increasing the stimulus input and increasing the processing steps required by the task led to a BDA. Thus, a BDA may be observed when a specific processing stage is loaded, either by increasing numbers of stimuli to be processed or by increasing the difficulty of a specific stimulus processing step, or a BDA may be observed because additional processing steps, distributed over the hemispheres, have to be carried out. Although we cannot rule out the latter explanation completely, because name matching led to increased activation in a bilateral network of anterior brain areas, compared to letter shape matching, the same was true for the reverse contrast, for letter shape–name matching. Thus, the evidence for an explanation of the BDA in letter name matching in terms of distribution of multiple processes over the hemispheres is compara-

tively weak, whereas there is clear evidence for an explanation of the BDA in terms of interhemispheric resource sharing due to increased demands on a specific processing stage, in this case visual letter processing.

Brain areas involved in interhemispheric transfer

Bilateral matches have the potential advantage that both hemispheres can initially process part of the information, in this way sharing their resources. This may be advantageous when a single hemisphere on its own reaches its resource limits. In contrast, as long as resource limits are not yet reached, unilateral matches may be advantageous, because both letters are directly channeled to one hemisphere, which then can carry out the matching operation. In this case, bilateral input carries the additional burden that the nature of at least one of the letters needs to be signaled via callosal fibers so that both letters can be compared.

This kind of reasoning is consistent with the pattern of activation found in anterior and posterior cingulate cortices. Both showed an interaction of task \times visual hemifield of presentation. This interaction was due to an increased activation for bilateral shape matches over bilateral name matches, whereas there was no difference in the activation elicited by unilateral name and shape matches.

Since the activation data from the occipital visual areas indicate consistent bilateral processing for name matches, but processing restricted to the hemisphere of input in shape matches, the pattern of activation reflects precisely the amount of interhemispheric transfer in the different conditions. ACC-complex activation was previously found with divided attention demands (Corbetta et al. 1991; Pollmann et al. 2000b). In the monkey, both ACC complex and posterior cingulate/retrosplenial cortex are connected to each other (Morris et al. 1999a, 1999b). Our data show that they may be involved in different aspects of a common goal, the exchange of information between the hemispheres.

Cingulate activation was especially strong for bilateral shape matching, leading to a significant main effect of task (see below). In our interpretation, this means that interhemispheric transfer is especially costly in bilateral shape matching. A previous study comparing three and four letter displays may support this interpretation. Compared to a three-letter display, in which a single bottom item had to be compared to two top items (one in each VF), the cost of between-field shape matching increased sharply (from 18 ms to 183.5 ms) when two bottom items were presented and subjects had to decide whether either matched one of the top items (Weissman et al. 2000). The BDA for name matching remained almost the same (three-item displays: 55 ms, four-item displays: 41 ms).

Letter name versus letter shape matches

Letter name matching, compared to matching of physical letter shape, selectively activated a network of brain areas which was lateralized to the left hemisphere in posterior cortex, but distributed bilaterally in frontal cortex. One prominent activation was observed in the inferior occipital gyrus, at the border to the temporal lobe. The location of this activation was almost identical to a location reported by Puce et al. (1996) to be activated more strongly by presentation of letter strings than of faces or random textures. It may seem puzzling that the strongest name-match specific activation was observed in a brain area which subserves visual letter processing, rather than an area involved in phonological processing. However, it is easy to see that the matching of different shapes belonging to the same letter (such as A–a) may pose higher demands on visual letter processing than a physical identity match (A–A).

Name matching also elicited a chain of activations along the left intraparietal sulcus. These activations resemble those found in previous studies of visuospatial selective attention. However, there is no reason to believe that visuospatial demands were any different between name and shape matching; we rather interpret our data as evidence for the global attentional function of the cortex along the intraparietal cortex (Wojciulik and Kanwisher 1998). The activation along the posterior segment of the intraparietal sulcus coincides with the area Simon et al. (2002) found activated in a word decision task which afforded orthography to phonology conversion. Clearly, the same process may be at work in letter name matching.

The bilateral frontal activations at the junction of the inferior frontal and inferior precentral sulci may represent the higher executive task demands posed by letter name matching, compared to shape matching (Mecklinger et al. 2000). Name matching also elicited an activation in right frontopolar cortex. This area has often been reported to support retrieval processes (Buckner et al. 1995, 1998; Squire et al. 1992). Since letter name matching is distinct from letter shape matching in that the letter identity has to be accessed, it may be that right frontopolar cortex supports retrieval of letter identity from semantic memory in name matching.

Interestingly, there was also a network of areas which was selectively activated by letter shape matches, compared to letter name matches. This shows that the additive factors logic, which views letter name matching as a composition of basic letter perception processes, which are shared with letter shape matching, plus additional lexical processing steps, is too simplistic.

Letter shape matching selectively activated the posterior parts of the superior temporal gyri, which have previously been reported in a task of visuospatial cueing (Nobre et al. 1997). It further activated parts of the superior frontal gyri, which we and others have found active in tasks with high demands both on visuospatial attention and target discrimination (Hopfinger et al. 2000; Weidner et al. 2002). The need to discriminate between alternative targets was

also a task characteristic of the study by Nobre et al. (1997), but in this study the discrimination (between a + and an x) was rather easy. Thus the activation obtained for letter shape matching may reflect brain areas specifically involved in shape discrimination. Although shape discrimination is also needed for letter name matching, the instruction to match letters by shape may enhance these processes.

Bilateral versus unilateral matches

Contrasting bilateral minus unilateral matches across tasks elicited only a few activations. For one, bilateral matches activated striate (and possibly parts of peristriate) cortex more than unilateral matches. This is an interesting finding, because the physical stimulus display was the same for unilateral and bilateral matches, with two letters being presented in both hemifields. The only difference was the position of the cues, and it is not obvious how their physical presence should lead to stronger activation in the bilateral case. (By the same logic, two cues in one hemifield, e.g., the LVF, in unilateral matching, compared to one cue in each hemifield, as in bilateral matching, might lead to increased activation in contralateral cortex, e.g., the RH). Thus, we interpret the increased striate activation for bilateral matches as an attentional modulation effect, which results from attending to both halves of the display in bilateral matches, versus attending to one-half of the display in unilateral matches. The interpretation as an attentional modulation may be supported by the observed asymmetry of the activation, which was stronger in the left hemisphere. This cannot be explained by any differences in the physical stimulus parameters between hemifields, but may rather be due to the left-hemispheric dominance of letter processing, which is apparent from previous reports (Puce et al. 1996; Polk et al. 2000) as well as the present data. This would mean that the lexical nature of the task leads to lateralized attentional modulation all the way down to V1.

An activation was further found at the horizontal segment of the right intraparietal sulcus. This may support a long-standing theory that right parietal cortex is specifically capable in attending to ipsi- as well as contralateral stimuli (Mesulam 1981; Heilman and Valenstein 1979). An alternative interpretation may be that this activation reflects an enlargement of the attentional focus in the bilateral compared to unilateral matching tasks, which may become necessary because the cued positions are more distant in the former. However, this remains speculative for two reasons: (1) to our knowledge, the functional neuroanatomy of focus size adjustments has not been firmly established; and (2) there is a debate whether attention can be focussed independently on two distant locations independently or not (Castiello and Umiltà 1992; McCormick et al. 1998). More recent studies on object-based attention, however, have shown that attention indeed can be allocated to several independent objects (OGrady and Mueller 2000). A further activation was observed in

anterior cingulate cortex. This area was most strongly activated by bilateral shape matches, as discussed in relation to the task \times VF interaction above.

Conclusions

In conclusion, we found that unilateral, compared to bilateral, letter name matches led to increased activation in the contralateral fusiform and lateral occipital gyri. These signal increases, in turn, went along with ipsilateral activation of functionally homologous areas. In letter shape matching, both of these effects were absent. We interpret this pattern of activation as hemispheric resource sharing, which occurs when the hemisphere of input reaches its resource limits.

Interhemispheric resource sharing in name matching, but not in shape matching, implies lower demands on interhemispheric transfer in bilateral than unilateral name matches. The absence of interhemispheric resource sharing in shape matching implies the opposite: Higher demands on bilateral compared to unilateral shape matches. The pattern of activation in the anterior and posterior cingulate cortices reflects these differences in interhemispheric transfer. These areas may thus be involved in the coordination of interhemispheric transfer.

Acknowledgements We would like to thank B. Reimann, M. Weigl and M. Maertens for assistance in programming and running experiments and data analysis and two anonymous reviewers for valuable comments. This work was supported by USPHS grant NS20187 to E.Z. and DFG grant PO 548/3-1 to S.P.

References

- Banich MT (1998) The missing link: the role of interhemispheric interaction in attentional processing. *Brain Cogn* 36:128–157
- Banich MT, Belger A (1990) Interhemispheric interaction: how do the hemispheres divide and conquer a task? *Cortex* 26:77–94
- Belger A, Banich MT (1992) Interhemispheric interaction affected by computational complexity. *Neuropsychologia* 30:923–931
- Belger A, Banich MT (1998) Costs and benefits of integrating information between the cerebral hemispheres: a computational perspective. *Neuropsychology* 12:380–398
- Bosch V (2000) Statistical analysis of multi-subject fMRI data: assessment of focal activations. *J Magnet Reson Imag* 11:61–64
- Buckner R, Petersen S, Ojemann J, Miezin F, Squire L, Raichle M (1995) Functional anatomical studies of explicit and implicit memory retrieval tasks. *J Neurosci* 15:12–29
- Buckner R, Koutstaal W, Schacter D, Dale A, Rotte M, Rosen B (1998) Functional-anatomic study of episodic retrieval: II. Selective averaging of event-related fMRI trials to test the retrieval success hypothesis. *Neuroimage* 7:163–175
- Castiello U, Umilta C (1992) Splitting focal attention. *J Exp Psychol Hum Percept Perform* 18:837–848
- Copeland SA (1995) Interhemispheric interaction in the normal brain: comparisons within and between the hemispheres. PhD dissertation, Department of Psychology, University of California at Los Angeles
- Copeland SA, Zaidel E (1996) Contributions to the bilateral distribution advantage. *J Intl Neuropsychol Soc* 2:29
- Corbetta M, Miezin FM, Shulman GL, Petersen SE (1991) Selective and divided attention during visual discriminations of shape, color, and speed: functional anatomy by positron emission tomography. *J Neurosci* 11:2383–2402
- Eviatar Z, Zaidel E (1994) Letter matching within and between the disconnected hemispheres. *Brain Cogn* 25:128–137
- Friston KJ, Holmes AP, Worsley KJ, Poline JB, Frith CD, Frackowiak RSJ (1995) Statistical parametric maps in functional imaging: a general linear approach. *Hum Brain Mapp* 2:189–210
- Friston KJ, Williams S, Howard R, Frackowiak RSJ, Turner R (1996) Movement-related effects in fMRI time-series. *Magnet Reson Imag* 35:346–355
- Friston KJ, Zarahn E, Josephs O, Henson RNA, Dale AM (1999) Stochastic designs in event-related fMRI. *Neuroimage* 10:607–619
- Heilman KM, Valenstein E (1979) Mechanisms underlying hemispatial neglect. *Ann Neurol* 5:166–170
- Hopfinger JB, Buonocore MH, Mangun GR (2000) The neural mechanisms of top-down attentional control. *Nat Neurosci* 3:284–291
- Josephs O, Henson RN (1999) Event-related functional magnetic resonance imaging: modelling, inference and optimization. *Philos Trans R Soc Lond B Biol Sci* 354:1215–1228
- Loftus GR, Masson MEJ (1994) Using confidence intervals in within-subject designs. *Psychon Bull Rev* 1:476–490
- Lohmann G, Mueller K, Bosch V, Mentzel H, Hessler S, Chen L, von Cramon DY (2001) Lipsia—a new software system for the evaluation of functional magnetic resonance images of the human brain. *Comput Med Imaging Graph* 25:449–457
- McCormick PA, Klein RM, Johnston S (1998) Splitting versus sharing focal attention: comment on Castiello and Umilta (1992). *J Exp Psychol Hum Percept Perform* 24:350–357
- Mecklinger A, Bosch V, Gruenewald C, Bentin S, von Cramon DY (2000) What have Klingon letters and faces in common? An fMRI study on content-specific working memory systems. *Hum Brain Mapp* 11:146–161
- Mesulam MM (1981) A cortical network for directed attention and unilateral neglect. *Ann Neurol* 28:597–613
- Morris R, Pandya DN, Petrides M (1999a) Fiber system linking the mid-dorsolateral frontal cortex with the retrosplenial/presubicular region in the rhesus monkey. *J Comp Neurol* 407:183–192
- Morris R, Petrides M, Pandya DN (1999b) Architecture and connections of retrosplenial area 30 in the rhesus monkey (*Macaca mulatta*). *Eur J Neurosci* 11:2506–2518
- Nobre AC, Sebestyen GN, Gitelman DR, Mesulam MM, Frackowiak RS, Frith CD (1997) Functional localization of the system for visuospatial attention using positron emission tomography. *Brain* 120:515–533
- OGrady RB, Mueller HJ (2000) Object-based selection operates on a grouped array of locations. *Percept Psychophys* 62:1655–1667
- Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9:97–113
- Polk T, Farah M (2002) Functional MRI evidence for an abstract, not perceptual, word-form area. *J Exp Psychol Gen* 131:65–72
- Pollmann S, Dove A, von Cramon DY, Wiggins CJ (2000a) Event-related fMRI: comparison of conditions with varying BOLD-overlap. *Hum Brain Mapp* 9:26–37
- Pollmann S, Weidner R, Müller HJ, von Cramon DY (2000b) A fronto-posterior network involved in visual dimension changes. *J Cognit Neurosci* 12:480–494
- Posner MI (1969) Abstraction and the process of recognition. In: Bower GH (ed) *The psychology of learning and motivation*, III. Academic, New York
- Puce A, Allison T, Asgari M, Gore JC, McCarthy G (1996) Differential sensitivity of human visual cortex to faces, letterstrings and textures: a functional magnetic resonance imaging study. *J Neurosci* 16:5205–5215

- Simon O, Mangin JF, Cohen L, Le Bihan D, Dehaene S (2002) Topographical layout of hand, eye, calculation, and language-related areas in the human parietal lobe. *Neuron* 33:475–487
- Squire L, Zola-Morgan J, Amaral DG, Winters BD, Bussey TJ, Saksida LM, Bussey TJ, Bussey TJ, Bussey TJ (1992) Activation of the hippocampus in normal humans: a functional anatomical study of memory. *Proc Natl Acad Sci U S A* 89:1837–1841
- Talairach J, Tournoux P (1988) *Co-planar stereotaxic atlas of the human brain*. Thieme, Stuttgart
- Weidner R, Pollmann S, Müller HJ, von Cramon DY (2002) Top-down controlled visual dimension weighting: an event-related fMRI study. *Cereb Cortex* 12:318–328
- Weissman DH, Banich MT (2000) The cerebral hemispheres cooperate to perform complex but not simple tasks. *Neuropsychology* 14:41–59
- Weissman DH, Banich MT, Puente EI (2000) An unbalanced distribution of inputs across the hemispheres facilitates inter-hemispheric interaction. *J Int Neuropsychol Soc* 6:313–321
- Wojciulik E, Kanwisher N (1998) The generality of parietal involvement in visual attention. *Neuron* 23:747–764