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**Interhemispheric interaction
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1 Introduction

The question of hemispheric differences and hemispheric communication is still a matter of debate and interest as it has been for many years. Evidence for hemispheric differences comes from very early lesion studies and received new interest with the groundbreaking research of so-called split-brain patients, for which Roger Sperry achieved the Nobel Prize in 1981. Recently, the use of new methods like functional imaging has further enlightened processing differences between the two cerebral hemispheres. While this body of research is focussing mainly on hemispheric differences and lateralization of functions, usually both hemispheres are able to carry out the task relevant processes, and the two hemispheres work together, not independently. Interhemispheric interaction has been observed on a variety of different tasks, and different patterns of interaction can be explained by different models of hemispheric communication. Generally, in the patterns of cerebral cooperation and communication, it has often been demonstrated that the whole is different from the sum of its parts.

This dissertation examines hemispheric differences and hemispheric interactions at the stage of high-level visual processing. It will focus on activation differences in regions of the occipitotemporal cortex particularly involved in the visual processing of pictures of different categories and of stimuli with different formats. With the use of new functional imaging methods, it has consistently been demonstrated that pictures of faces and buildings elicit specific peaks of activation in temporal-occipital regions, and written words typically elicit activation at the left fusiform

gyrus/lateral occipital sulcus. Although this pattern of activations has been replicated in numerous studies, the response properties of these object- and word-specific visual areas in terms of visual hemifield effects are rarely investigated. This will be the main aim of this dissertation. Pictures of faces and buildings along with words naming those pictures will be presented in lateralized displays and effects of hemispheric specialization and interaction will be investigated under different task and stimulation conditions.

Another aspect, although not the main focus, will be the response of object-selective areas to words naming preferred and unpreferred pictures. Since pictures and their written names are used within the same experiment, common influences on activation in object-selective areas need to be considered.

The outline of this dissertation is as follows. In the next chapter 'Object selective areas', I will selectively review the current status of research on object-selective areas with a focus on the three areas especially relevant for the following experiments: the fusiform face area (FFA), the parahippocampal place area (PPA), and the visual word form area (VWFA). Their general response properties and functional roles will be discussed in the frame of different models on the organization of the human visual system. Furthermore, lateralization effects in behavioral and imaging measures will be evaluated.

In the following chapter 'Models and data on interhemispheric processing', different models on interhemispheric cooperation along with associated findings will be discussed. I will address the issue of hemispheric specialization with respect to general models of hemispheric cooperation and findings specifically related to visual word processing and object recognition.

The fourth chapter is dedicated to methodology and will focus primarily on the divided visual field paradigm and functional magnetic resonance imaging, methods most relevant for the experiments of this dissertation.

Chapter five to nine report and discuss the four fMRI-experiments. Their results will be summarized and integrated in the general discussion of chapter ten leading to the general conclusion and future prospects.

2 Object Selective Areas

For a better understanding of how the object-selective areas can be integrated in visual processing, I will first briefly describe general principles of organization and function in the human visual system. Human primary visual cortex (V1) is located at the occipital pole of each hemisphere and falls mostly in the calcarine sulcus. Early visual areas are organized topographically, i.e. information from points of adjacent retinal location are processed by adjacent neurons. Furthermore, the mapping of retinal location to cortical location is based on two dimensions: eccentricity and polar angle. Eccentricity refers to the shift from central to peripheral visual field representation along the posterior to anterior direction in the calcarine sulcus. Polar angle refers to the representation of the distance from the horizontal median, where different degrees (i.e. a rotation from the upper to the lower vertical meridian) are represented in a shift from the lower to the upper lip of the calcarine sulcus (see Wandell, 1999 for a review).

As one general ordering principle, visual perception is organized hierarchically, i.e. low level inputs are transformed into abstract representations in a series of processing stages. For example, V1 neurons respond selectively to stimulus orientation, while neurons further along the occipito-temporal pathway respond to general object shapes. However, visual processing is not only determined by these bottom-up processes, but is also modulated by top-down influences (see Grill-Spector & Malach, 2004 for a recent review).

Along with the hierarchical organization, two functionally different processing streams can be distinguished: the ventral and the dorsal stream. The ventral 'what' stream consists of occipito-temporal cortical regions and appears to be involved mostly in object recognition and perception (Mishkin et al., 1983). The dorsal 'action' (Goodale et al., 1991), originally labeled 'where' (Mishkin et al., 1983), stream consists of an occipital-parietal pathway and is mainly involved in visually-guided actions (e.g. Ungerleider & Haxby, 1994). Within the ventral visual pathway, functional imaging studies have shown that regions in the occipito-temporal cortex respond preferentially to pictures of specific types of objects. Similarly, written words elicit specific regions supposedly at a comparable visual processing stage. These regions are functionally located at a stage of higher visual processing, i.e. pictures of certain categories activate these areas independently of the pictures' low-level stimulus features or its retinal location. These areas are referred to as object-selective areas, although selectivity in this sense is always relative, not absolute. Different object-selective areas and their response properties, specifically related to visual hemifield effects, will be investigated in this dissertation, namely the parahippocampal place area, the fusiform face area, and the visual word form area. The following chapters will refer and discuss relevant findings and theoretical models that have been suggested for the functional role of these areas in the general organizational principle of the human visual system.

2.1 Parahippocampal Place Area and Fusiform Face Area

The most prominent examples for categories that have been reported to elicit activation of specific areas in the occipito-temporal

areas, which will be specifically investigated in this dissertation, are faces, houses (or scenes) and words. Other examples include animals, tools (Chao et al., 1999), chairs (Ishai et al., 2000), and body parts (Downing et al., 2001). More specifically, it has been demonstrated that an area in the medial/lateral fusiform gyrus, the fusiform face area (FFA; Kanwisher et al., 1997), is more strongly activated when subjects view pictures of faces in comparison to viewing scrambled pictures or pictures of other objects (e.g. Chao et al., 1999; Gauthier et al., 2000; Haxby et al., 1999; Ishai et al., 2000; Puce et al., 1995; 1996, Spiridon et al., 2006, Xu, 2005). In some studies, a more posterior region sometimes called the occipital face area was additionally found (OFA, e.g. Rossion et al., 2003a). In contrast, pictures of buildings specifically activate a region in the parahippocampal/lingual gyrus (e.g. Aguirre et al., 1998a; Haxby et al., 1999, Ishai, 2000; Spiridon & Kanwisher, 2002, Tong et al., 2000), which has been called parahippocampal place area (PPA, Epstein & Kanwisher, 1998). Similar, but maybe not identical, regions are activated by spatial layouts, such as scenes (Epstein et al., 1999). Responses of the FFA and the PPA to different stimulus conditions will be investigated in this dissertation in event-related functional imaging experiments to examine effects of hemispheric interaction at this processing level. Following the literature, I will use the terms FFA and PPA in the remainder of the dissertation. However, this does not imply a specific theoretical statement of their functionality. Different models exist with regard to the function of these areas (see next chapter).

To rule out that greater responses to pictures of certain categories are based on stimulus features other than depicting an image of a certain category, several control conditions have been used as a reference baseline in functional imaging studies. For example,

pictures of faces elicited stronger responses in the FFA compared to pictures with the same low-level stimulus features, e.g. luminance or contrast (e.g. Puce et al., 1996). Additionally, the FFA responded with a lesser degree to pictures containing only single face-specific features, e.g. only eyes or schematic faces, than to photographs of complete faces (Tong et al., 2000). However, activation in face specific regions of the middle fusiform gyrus proved to be invariant to changes of the spatial frequency composition of the faces depicted (Eger et al., 2004).

Similarly, the PPA responded more strongly to pictures of buildings than to scrambled versions of the same pictures. Scrambling pictures preserves some of their stimulus features, e.g. the average lightness (e.g. Epstein & Kanwisher, 1998). The strong response of the PPA to pictures of scenes and layouts was independent of familiarity of those scenes (Epstein et al., 1999), i.e. appears to be unrelated to the availability of memory episodes related to this environment. PPA responses did not generalize to other large-size objects such as airplanes or ships (cf. Epstein, 2005) and cars (Aguirre et al., 1998a). Even though the PPA might be relevant for navigation (Epstein, 2005), activation is elicited automatically during the visual processing of the preferred pictures, i.e. not restricted to tasks demanding actual mental navigation.

Pictures of faces and buildings will be used in the three experiments of this dissertation to identify the FFAs and PPAs, respectively. Pictures will show different exemplars with the same basic features (for example with respect to visible facial features, see method section for details). Therefore, activation differences based on inter-categorical stimulation should be small and will be further controlled by balancing stimulus presentation across conditions. Scrambled versions of those pictures will be used as

control condition of visual stimulation. Scrambled pictures should be processed in the same way as the pictures during early visual processing stages, but do not contain any categorical information.

An additional strong argument against the alternative explanation that selective responses of these areas are driven by different physical stimulus characteristics is made by the observation of increased FFA and PPA activation when subjects actually see a face or a building compared to conditions of identical visual stimulation but without the subjective percept. This was demonstrated, e.g. during binocular rivalry, for ambiguous pictures like the face-vase illusion, or when attention was switched between categories while viewing superimposed pictures (Andrews & Schluppeck, 2004; Hasson et al., 2001; Serences et al., 2004; Tong et al., 1998).

Areas of strongest activation respond selectively, but not exclusively, to pictures of the preferred object-category. For example, the FFA was also activated by pictures of body parts or pictures of animals, but to a lesser degree. Similarly, the PPAs responded to furniture or other large objects, but much stronger to pictures of scenes and buildings (e.g. Kanwisher, 2003). It was proposed that a criterion for selectivity is met, if the signal increases in functional magnetic resonance imaging (fMRI) are at least twice as large in response to pictures of a preferred category compared to pictures of any other object category (e.g. Kanwisher et al., 2003, but see Chao, et al., 1999).

Another question concerns the specificity of the response, which could further indicate the level of processing occurring in those areas. To test if the response in object-selective areas is sensitive to changes of size, position, etc., effects of fMRI adaptation mechanisms can be utilized (Grill-Spector & Malach, 2001). If a region is insensitive to a certain feature, it will show adaptation

effects throughout changes of this feature. For example, if identical objects are repeatedly presented, the fMRI signal decreases over time in object-related visual areas. A signal increase in these areas is subsequently observed for the presentation of different objects, but not for the presentation of the same objects in a different visual format (e.g. photographs versus line drawings; see Grill-Spector et al., 2001 for a review). This difference in recovery from adaptation can be interpreted as sensitivity and insensitivity for exemplar and format of objects in those areas, respectively.

Studies examining the viewpoint-specificity of responses to faces and scenes in the FFA and PPA have yielded mixed results. In posterior (Grill-Spector et al., 1999) and lateral regions of the fusiform gyrus (Pourtois et al., 2005), no adaptation to changes in viewpoint for otherwise identical pictures of faces and buildings was observed, indicating viewpoint-specificity. On the other hand, medial regions did show viewpoint-independency for pictures of unfamiliar faces (Pourtois et al., 2005). Scene processing in the PPA appeared to be viewpoint-specific in one study, although the response was less sensitive to object changes within the general layout (Epstein et al., 2003). The opposite effect of viewpoint-independence, however, was obtained in another study (Ewbank et al., 2005). The spatial resolution of fMRI might have constrained the ability to detect subtle activation changes during viewpoint changes. In face specific cells of the monkey inferotemporal cortex, a selective activation for faces with different degrees of rotation was found, covering a cortical area of only about 1 mm² in size (Wang et al., 1996).

The exact neuronal representation of faces in the FFA and buildings in the PPA is still unclear. Recently, psychophysiological and functional imaging evidence suggests that faces are represented in a multidimensional space where individual faces are

defined by their distance from a mean face (Leopold et al., 2001; Loffler et al., 2005).

Along with possible activation changes based on different stimulation with preferred and unpreferred categorical information in the ipsi- and contralateral visual hemifield, responses of the object-selective areas can additionally be modulated by top-down processes (e.g. Mechelli et al., 2003). In the experiments of this dissertation, top-down influences will mainly be investigated in the response of the object-selective areas to words naming preferred and unpreferred pictures, because activation of FFAs and PPAs is possible without perceptual stimulation with pictures of faces and buildings at all, i.e. during visual imagery (Ishai et al., 2002; O'Craven & Kanwisher, 2000). Variations of task demands can also lead to an increase in top-down influences. For example, attending to objects of certain categories can lead to a selective activation increase in the respective object-selective areas (e.g. O'Craven et al., 1999; Tong et al., 1998). Enhanced activation has also been reported during object-specific working memory rehearsal (O'Craven et al., 1999; Druzgal & D'Esposito, 2001, 2003; Ranganath et al., 2004a, 2004b; Serences et al., 2004).

2.2 Functional Role of FFA and PPA

2.2.1 Function in Object Recognition

Although it is not the main focus of this dissertation to specifically test different hypotheses related to the functional significance of activation in object-selective areas for object recognition or object representation, I will report the main theoretical considerations, because determining the response properties of the FFA, PPA, and VWFA to various conditions of ipsi- and contralateral stimulation,

and to different conditions of categorical information helps to further characterize the processing level and general functionality of these areas (Niemeier et al., 2005; Vigneau et al., 2005).

Generally, the functional significance of object-selective areas for object recognition is still under debate. For example, it has been suggested that the FFA is mainly involved in face detection (Tong et al., 2000), but there is also evidence for an FFA involvement in higher processes (Bruce & Young, 1986) like face recognition and face identification. Similarly, an involvement of the PPAs for scene and place recognition has been demonstrated. For example, in a detection task with pictures from different categories, subjects reported after each trial if they had recognized the presented picture at the level of exemplar identity (e.g. Harrison Ford; electric guitar), or only at the level of category identity (e.g. face or guitar, with an inability of individual identification), or if they did not recognize the specific object-category at all. Signal increases were observed in the respective object-selective areas for trials of correct category-detection as well as for trials of correct individual-identification, but not for trials of unsuccessful category identification (Grill-Spector, 2003). Interestingly, for corresponding pictures, the signal's amplitude for false alarms at the identity level was higher than the signal's amplitude for correct detection in their respective object-selective areas. Thus, the response of object-selective areas was stronger during correct category detection when subjects had an additional 'feeling' of correct identification at the individual level, even when this subjective impression was wrong.

Although this study provided evidence for stronger responses to stimuli identified at the individual level, FFA and PPA activation is not assumed to be involved in the representation of semantic information per se, e.g. for a famous person's or building's name

(Gorno-Tempini & Price, 2001; Haxby et al., 2000). However, as will be discussed in the context of Experiment 2, names of faces and buildings could lead to FFA and PPA activation, because of modulating top-down mechanisms (e.g. Mechelli et al., 2004). Other aspects of facial attributes that might be processed at different cortical locations include emotion and eye gaze (e.g. Hoffman & Haxby, 2000).

Additionally, even if corresponding to subjective experience, activation of object-selective areas is not sufficient to result in conscious perception. For instance, in a rapid serial visual presentation task, detection of a second target is impaired when it appears during a specific time window after the detection of a first target, the so-called attentional blink (AB). PPA activation was enhanced for second target trials when subjects made a correct judgment about the type of the scene presented, i.e. after a supposedly conscious detection. Still, PPA activation was stronger on trials where scenes were presented as second targets compared to no scene presentation at all, even when subjects had made an incorrect judgment about the scene, i.e. when it remained supposedly undetected (Marois et al., 2004).

Neuropsychological findings concerning the specific functional involvement of these areas in object recognition are ambiguous, too. A classic neuropsychological approach is, to associate a specific lesion side with a specific cognitive deficit. Ideally, a functional relation between cognitive processes and cortical areas is demonstrated via double-dissociation. If two patients suffer from different lesions and one patient can perform task A but not task B while the second patient shows the exact opposite pattern, i.e. can perform task B but not task A, it can be inferred that performance on both tasks is independent and that the relevant processing takes

place in separable cortical areas, namely somehow related to the respective lesion side of patient A and B. In the field of object recognition, it has been proposed that such a double dissociation exists with respect to face and object processing, which would demonstrate their independence. The selective inability to identify faces has been termed *prosopagnosia*, meaning face blindness. Since object recognition should be intact in patients suffering from prosopagnosia, a general visual deficit cannot account for the selective impairment of face recognition. Furthermore, patients suffering from prosopagnosia can recognize people via other cues, e.g. voice or gait, indicating that prosopagnosia is not a function of impaired memory functions per se. Some evidence from lesion studies suggests that damage at regions corresponding to the FFA indeed leads to prosopagnosia (Wada & Yamamoto, 2001) and that cortical damage at the location of the PPAs results in recognition deficits relative specific for buildings (landmark agnosia, Aguirre & D'Esposito, 1999). However, there is still an ongoing debate about cortical lesions necessary and/or sufficient for prosopagnosia to occur (e.g. Rossion et al., 2003a), along with the question of how selective for faces the recognition deficit really is (e.g. Gauthier et al., 1999a).

2.2.2 Function in General Organization of Visual Cortex

Above and beyond the question of their functionality in object recognition as such, the role of object-selective areas has also been discussed with respect to more general models of visual object representation. One critical issue of disagreement between different models of functional organization is the question of parcellation: at one end of the continuum, areas most strongly activated by a certain category reflect specific and exclusive modules for their respective

recognition (e.g. Kanwisher et al., 1997; Andrews & Schluppeck, 2004). In addition to highly specialized modules for a subset of categories, like the FFA and PPA, objects from all other categories are recognized by an unspecific system. At the other end of the continuum, it has been suggested that the peaks of activation in specific cortical areas do not contain any category-specific information at all. Instead, in these models object representation is thought to be distributed and overlapping across the entire occipito-temporal cortex (e.g. Haxby et al., 2001; Ishai et al., 1999, 2000).

To support the modular view, behavioral and neuropsychological findings have been cited confirming the assumption that face-processing involves specific mechanisms. Examples include the face-inversion effect in the behavioral, and cases of supposedly pure prosopagnosia in the neuropsychological domain. The face inversion effect is characterized by distortions of face recognition for inverted (i.e. upside down) pictures of faces. This sensitivity to an upright orientation appears to be more specific for the recognition of faces than for the recognition of any other object (Yovel & Kanwisher, 2004; see Kanwisher, 2000 for a review). Consistent with the distributed view, category-specific activation patterns were observed in voxels throughout the occipito-temporal cortex, although the distribution was more concentrated for faces (Ishai et al., 2000). Furthermore, cross-correlating the activation strength of voxels from the entire temporal-occipital cortex, within category correlations were still higher than across category correlations even when voxels maximally activated by that category were excluded from the analysis. Thus, categories could still be discriminated based on the information contained in the responses of voxels preferring different categories (Haxby et al., 2001; but see Spiridon & Kanwisher, 2002).

Others have suggested that especially the right-hemispheric FFA activation is not related to face processing per se, but reflects a general processing mechanisms of objects at the individual level. Faces would provoke identification at the individual level automatically, but any other object could initiate the same type of processing if the required degree of expertise is available. Accordingly, right hemispheric activation at a location comparable to the FFA was found for car, bird or 'Greeble' experts for pictures of their respective expertise. 'Greebles' are artificial objects for which, consistent with the expertise hypothesis, FFA activation was found only after extensive training when a high level of expertise was reached and individual Greeble identification was as fast as the more general category detection. In the functionally defined right FFAs, signal increases were also observed for stimuli of the respective expertise (Gauthier et al., 1999b, 2000; Tarr & Gauthier, 2000; see Xu, 2005 for a recent review). The process-based view has been challenged, for example, because of dissociations between face and Greeble recognition observed in agnostic patients, which was interpreted as evidence for different underlying mechanisms (Duchaine et al., 2004). Due to their opposing views, arguments in favor of modular face processing also argue against the expertise hypothesis and vice versa.

Along with the assumption that object-selective areas are derived from different types of processing rather than from different types of categories, it has been hypothesized that processing differences reflect a more general organizational principle throughout the visual cortex. Objects requiring high-detailed analyses (e.g. faces) are associated with central visual field representation, while objects requiring large-scale integration (e.g. places) are associated with peripheral visual field representation. These resolution demands are

the underlying principle of the typical spatial layout of lateral-to-medial topography for the FFA and PPA (Hasson et al., 2002, 2003; Levy et al., 2001; Malach et al. 2002). A similar association to central visual field representation was found for another group of stimuli requiring detailed visual discrimination, i.e. letter strings and words (Hasson et al., 2002). The assumption that object-selective areas are cortically arranged based on underlying processing requirements, however, does not rule out the possibility that these processing differences are still specific for certain categories.

In summary, the organization of the visual system with respect to the function of object-selective areas is still under debate. Some of the above mentioned models are mutual exclusive, e.g. the propositions of modular versus distributed object processing. Other models, however, are compatible with each other, e.g. accounts based on eccentricity and processing demands. Generally, even though their functional role is still questioned, the topography of category-specific areas is replicable across and within individuals over time and in a variety of different paradigms (Cohen & Dehaene, 2004; Malach et al., 2002; Peelen & Downing, 2005; Spiridon et al., 2006, but see next chapter for possible differences in the degree of lateralization for the FFA).

2.3 Visual Word Form Area

Along with temporal and inferior frontal areas typically involved in word reading (see Jobard et al., 2003 for a review), printed words and pseudowords consistently activate left-hemispheric areas in the middle fusiform gyrus relative to non-linguistic visual stimulation as textures or pictures of faces (Price et al., 1996; Puce et al., 1996). The stronger response of this area to consonants than to digits demonstrates that the response is not based on low-level visual

features, e.g. patterns of edges and shapes, but specific to letters (Polk et al., 2002). Written words and pseudowords consistently activate an area of the left lateral occipital sulcus/middle fusiform gyrus, which has been labeled 'Visual Word Form Area' (VWFA, Cohen et al., 2000, 2002; Cohen & Dehaene, 2004). The labeling has subsequently been challenged, particularly because the proposed specificity for written language has been questioned (Price & Devlin, 2003, 2004). It has been argued that activation in this area was also found for semantic processing of pictures (Bookheimer et al., 1995), during auditory word processing (Price & Devlin, 2003), and during Braille reading (Büchel et al., 1998; but see Cohen et al., 2004).

Functionally, the VWFA supposedly extracts an abstract letter identity that is invariant of visual features (Dehaene et al., 2002). Accordingly, activation of this area is independent of letter cases and of perceptual familiarity (Dehaene et al., 2001; Polk & Farah, 2002). Processing words at this level of visual analysis appears to occur automatically even under conditions of unconscious perception. Both, masked and unmasked words elicited VWFA activation, although the increase was considerably smaller during masked trials (Dehaene et al., 2001). While extraction of an abstract letter identity reflects prelexical visual stages of word reading (Dehaene et al., 2002), others have suggested that the VWFA is instead involved in binding visual and verbal associations of words (Vigneau et al., 2005), or is located at later lexical processing stages (Kronbichler et al., 2004). A recent magnetoencephalographical (MEG) study has also proposed that VWFA activation occurs at later stages of processing (about 500ms after word presentation) and is perhaps even preceded by phonological processing (Pammer et al., 2004).

Consistent with a prelexical function of abstract word processing carried out in the VWFA, lesions (Cohen et al., 2003) or deafferentation (Molko et al., 2002) of the VWFA causes *pure alexia*, a neuropsychological deficit where patients are unaffected in their writing and spelling abilities, but have a specific reading deficit and can name written words only through a letter-by-letter identification strategy. A serial letter identification can (compensatively) be carried out in the right-hemispheric homologue (Cohen et al., 2004). In an acute state of stroke, however, patients with lesions at the VWFA location were mostly impaired on tasks requiring lexical output, i.e. reading and naming, and less in written word comprehension (Hillis et al., 2005).

As for the PPA and FFA, I will use the term VWFA throughout this dissertation without the implication of supporting all theoretical considerations associated to its original labeling.

2.4 Lateralization Effects: Behavioral and Functional Evidence

2.4.1 Object Processing

In this dissertation, activation differences in object-selective areas for contra- and ipsilateral stimulation with preferred and unpreferred categorical information will be investigated with fMRI. Pictures of faces and buildings will be presented lateralized, and information presented simultaneously in the opposite visual hemifield will be varied along different dimensions. Furthermore, the obtained behavioral data in two different tasks will be integrated into patterns of interhemispheric interaction.

In most studies, no differences have been reported in recognition and semantic categorization of pictures of objects between left and right visual hemifield presentations (Biederman & Cooper, 1991; Koivisto, 2000; Koivisto & Revonsuo, 2003a; Levine & Banich, 1982). A right-visual field advantage has been reported in some studies, but effects have been questioned based on methodological concerns (see Biederman & Cooper, 1991) and were sometimes very small in nature (8ms difference, McAuliffe & Knowlton, 2001). In accordance with the absence of lateralization effects in the behavioral data, activation in areas related to object recognition is typically observed bilaterally. High-order object areas are supposed to be non-retinotopic. Indeed, they are activated about equally strong during contra- and ipsilateral stimulation (Grill-Spector et al., 1998; Halgren et al., 1999). However, recently it has been reported that areas in the human lateral occipital complex show a relative preference for objects presented contralaterally (Niemeier et al., 2005).

Perceptual asymmetries have been investigated mostly with respect to face rather than building recognition. Some behavioral studies suggest that faces are identified faster when presented in the left than in the right visual hemifield (Dutta & Mandal, 2002; Levine et al., 1988; McCarthy et al., 1999; Rizzolatti et al., 1971; Young et al., 1985). A right hemisphere specialization for face recognition has also been inferred from chimeric face processing. Chimeric faces consist of two halves differing in at least one facial attribute and the perception of this facial attribute for the whole face, e.g. age, gender, and attractiveness, is more often based on the information contained in the left than in the right half-face (e.g. Burt & Perrett, 1997). This left-side bias, however, could also be due to an attentional preference of the left side (e.g. Phillips & David,

1997), because chimeric faces in those studies were often displayed under free viewing conditions, i.e. without the instruction to fixate.

Other studies, however, have failed to show any effects of visual hemifield on identification of pictures of faces (Basu & Mandal, 2004; Kampf et al., 2002). This absence of laterality effects was further supported by the results of a recent meta-analysis, where no consistent effect of a LVF advantage for face detection was obtained (Kampf et al., 2005). Overall, these results suggest that perceptual asymmetries cannot exclusively be determined by face-specific processing per se, but rather depend on the cognitive operations necessary for the task or depend on differences in stimulus or experimental variables (Compton, 2002; Nettleton & Bradshaw, 1983; Sergent, 1995). For example, Moscovitch et al. (1976) used a face matching task to determine whether perceptual asymmetries for faces occur at early or at later stages of the stimulus analysis. Subjects compared pairs of faces appearing in the right or left visual field either to each other or to a previously presented sample. Reaction times were shorter for faces presented in the LVF, but only when faces had to be compared to the memorized sample. No LVF advantage was obtained when faces had to be compared to each other. Similarly, faster reaction times to faces presented in the LVF were found only for a more complex memory search task, where subjects had to decide whether the presented stimulus was a member of an earlier learned set of stimuli or not. Again, no LVF advantage was observed in a less demanding, i.e. location discrimination, task (Schweinberger et al., 1994). The LVF advantage for face processing can therefore be considered as relative and dynamic rather than absolute. Generally, both hemispheres appear to be competent in processing pictures of

faces, with a task dependent relative right-hemispheric specialization.

In accordance with a behavioral LVF advantage for faces in some tasks, several imaging studies using fMRI and Positron Emission Tomography (PET) revealed stronger right- than left-hemispheric activation during processing of centrally presented pictures, although the degree of lateralization varied between studies (e.g. Kanwisher et al., 1997; Hasson et al., 2002; Druzgal & D'Esposito, 2003; Puce et al., 1996; Sergent et al., 1992). Sometimes, comparable to the behavioral data, no lateralization effects were reported, as well (e.g. Halgren et al., 1999; Peelen & Downing, 2005).

In electrophysiological studies, pictures of faces typically elicit a negative peak around 170ms after stimulus onset (the N170 component). The N170 has been found to show a small right lateralization effect as well (e.g. Rossion et al., 2003b; Tarkiainen et al., 2002; but see Linkenkaer-Hansen et al., 1998). The quantity of the N170 asymmetry was independent of the visual hemifield the face was presented in, i.e. it showed about the same amount of right-hemispheric lateralization during processing of half-faces in the LVF and RVF (Yovel et al., 2003). In accordance with the functional imaging data, it has been suggested that the posterior fusiform gyrus is the source location of the N170 (Rossion et al., 2003b; but see Itier & Taylor, 2004).

In MEG studies, sometimes bilateral symmetric responses were observed during face processing (Zouridakis, 1998), with no difference between ipsi- and contralateral face presentation (Liu et al., 2002). Consistent with a mixed pattern of lateralization findings in other paradigms and methods, a tendency for right hemispheric lateralization was observed in other studies (Halgren et al., 2000).

With respect to the PPA, a higher responsiveness towards peripheral stimulation was observed (Levy et al., 2004), but to my knowledge visual hemifield advantages have not been investigated. As reported in the previous chapter, pictures of buildings are usually presented centrally, which leads to bilateral PPA activation.

2.4.2 Word Processing

Lateralization effects in word processing have often been investigated in the more general field of hemispheric differences in linguistic competence (see also Chapter 3.4). In this context, different theoretical models of visual word recognition have been developed assuming either a different processing (e.g. Ellis, 2004) or a different representation of words in the left and right hemispheres (e.g. Paivio, 1991; Schwanenflügel, 1991; Beeman et al., 1994). An extensive review of the various theoretical models on linguistic processing in the left and right hemispheres is beyond the scope of this work. Instead, the discussion will be restricted to models and findings focusing on lateralization effects in visual word form processing.

In lexical decision tasks, where a briefly presented stimulus has to be classified as word or non-word, a RVF advantage is commonly reported (see Chiarello, 1988; and Querné et al., 2000 for overviews). A series of variables have been discussed to influence or to eliminate this difference in laterality, for example standard visual format (e.g. Ellis 2004; but see Jordan et al., 2003) and concreteness (see Fiebach & Friederici, 2004 for a review).

This behavioral RVF advantage is in accordance with the left-lateralized activation observed for the VWFA. Left-lateralized activation has been demonstrated in functional imaging not only during processing of centrally presented written words (e.g. Puce et

al., 1996; Hagoort et al., 1999; Polk et al., 2002), but also for words specifically presented in the ipsilateral LVF and contralateral RVF (Cohen et al., 2000). Indeed, it has been suggested that the behavioral advantage observed in lexical decision tasks is in fact based on hemispheric differences originating as early as the perceptual (i.e. prelexical) processing level (Whitney & Lavidor, 2005). Word stimuli in the right hemisphere are presumably processed only up to the level of V4. Information extracted at this processing stage (at a location invariant feature level) is then transferred to the left-hemispheric VWFA via the splenium of the corpus callosum (e.g. McCandliss et al., 2003; Molko et al., 2002). Therefore, bilateral or right-hemispheric activation can be expected at lower stages of visual processing with a shift towards the left hemisphere during increased lexical processing. Such patterns of results have been found in MEG (Tarkiainen et al., 2002) and fMRI studies (Tagamets et al., 2000). In electrophysiological studies (e.g. Khateb et al., 2001; Rossion et al., 2003b) a similar lateralization effect was found to occur around 150ms after stimulus presentation, probably originating from the occipito-temporal cortex. Consistent with a shift at later processing stages, earlier components indicative of lower visual processing levels were obtained bilaterally. However, recently a shift at later processing stages was observed in an fMRI study, because bilateral activation in a supposedly homologue right-hemispheric VWFA was found for pseudowords as well (Vigneau et al., 2005).

In accordance with the assumption of bilateral processing of visual feature analysis and left-lateralized processing of prelexical word-specific information, in patients with isolated callosal lesions, a pattern of reading comparable to pure alexia is restricted to words presented in the LVF. This is accompanied by an absence of the

left-lateralized VWFA activation for words presented ipsi-, but not contralaterally (Cohen et al., 2000).

As will be discussed in the chapter on hemispheric interaction, other models and data have suggested that words presented in the LVF are processed in the right hemisphere further than pre-lexical stages. This, however, might be a specific pattern occurring only during bilateral word stimulation (e.g. Schweinberger et al., 1994; see Chapter 3.3).

2.5 Summary and Implications for Present Experiments

The first chapter reviewed the literature on object-selective areas relevant for the following experiments. Pictures of faces and buildings as well as written words elicit activation in specific areas along the ventral visual stream. Activation of these areas, namely the FFAs, PPAs, and the VWFA, will be expected in all experiments, and pictures of faces and buildings, as well as written words will be presented to identify those areas.

While some response properties of these areas have been investigated, for example the specificity of the representation, effects of lateralized displays and hemispheric interaction at this level of visual processing are rarely reported. Using event-related fMRI and different stimulation conditions, these aspects will be investigated in this dissertation. It will be determined whether the FFA, PPA, and VWFA respond differently when preferred stimuli are presented ipsi- or contralaterally. Additionally, effects of congruent, incongruent, and unspecific categorical information in the opposite visual hemifield on activation in those areas will be differentiated. Furthermore, task demands will be varied to establish whether possible activation

differences are task specific or more general response properties of the FFA, PPA, and VWFA. Specifically, a category detection task and a semantic matching task will be used. For the category detection task, information can be processed independently in both hemispheres and the detection of a picture showing a face or a building, respectively, is sufficient to make the correct decision. For the semantic matching task, information needs to be integrated across both hemispheres and is presented in different formats, i.e. pictures and words. Different patterns of activation between the two tasks will reveal whether lateralization effects depend on the task, and whether the presence of written words change activation patterns of the relevant object-selective areas. Two experiments employing conditions of comparable shallow and deeper semantic processing will specifically investigate whether written names of the pictures also elicit category-specific responses in the respective object-selective areas. While no automatic effects of category-specific activation during word reading are expected, during more demanding tasks a category-specific effect for words could be observed based on top-down modulation of responses in the respective object-selective area, e.g. related to visual imagery.

Furthermore, differences in activation during conditions of uni- and bilateral stimulation can indicate variations of interhemispheric interaction patterns. This will be discussed in the next chapter.

3 Models and Data on Interhemispheric Cooperation

3.1 Hemispheric Communication

The left and right cerebral hemispheres are separated by the longitudinal fissure, but the two cerebral hemispheres are connected physically and functionally, mainly by the corpus callosum (CC), but also by the anterior and posterior commissures and subcortical fibers. The CC itself is organized topographically, i.e. frontal cortical areas are connected by more anterior fibers and posterior brain regions by more posterior fibers. The CC consists of four sections: rostrum, genu, body, and splenium (from rostral to caudal) and fibers from different parts transfer different types of information, for example, visual, somatosensory, and auditory (e.g. Funnell et al., 2000; Hoptman & Davidson, 1994).

An index of interhemispheric communication is the time needed for information to cross the CC, the *interhemispheric transmission time* (IHTT). IHTT is often assessed in the Poffenberger paradigm. In this paradigm, simple stimuli are briefly presented in the LVF or RVF and subjects have to indicate their presence with the additional manipulation of a response hand variation. Decision latencies are then compared between responses with the hand ipsi- and contralateral to the target to calculate the crossed-uncrossed difference (CUD). Commonly, the disadvantage of contralateral stimulation for the crossed condition, i.e. the duration of visuomotor information transfer from one hemisphere to the other, is on the

order of 4 ms (e.g. Weber et al., 2005b). In patients with callosal lesions, the IHTT is massively increased (see Hoptman & Davidson, 1994 for a review). IHTT and other measures of interhemispheric cooperation (redundancy gain, see next chapter) were uncorrelated within-subjects in a behavioral study (Corballis, 2002). Therefore, information transfer between the two hemispheres is likely to occur at different processing stages with different mechanisms under various task conditions.

Recently, it has been proposed that the CC is not only involved in 'simple' information transfer, but also in attentional control (Banich, 1998). Specifically, the CC supposedly plays an important role in the allocation of attentional resources, in a way that resources of both hemispheres are used best and that irrelevant information is filtered out at early stages of processing (Mikels & Reuter-Lorenz, 2004). Furthermore, the interhemispheric communication across the CC can be either excitatory or inhibitory between homologue areas of each hemisphere (see Bloom & Hynd, 2005 for a recent review).

In cases of otherwise untreatable epilepsy, the CC is cut to prevent seizures from spreading across the hemispheres. Patients who underwent this callosotomy have been termed *split-brain* patients. While it had originally been proposed that this surgery did not result in significantly qualitative changes of behavior, a series of studies with more sensitive paradigms revealed striking demonstrations of hemispheric specialization corroborating the importance of hemispheric communication on many different tasks (see Gazzaniga, 2000; 2005 for reviews).

3.2 Redundant Targets Effect

Bilateral stimulus presentation will be investigated in two different experimental paradigms in this dissertation. Firstly, bilateral picture

presentation will be investigated in a target detection task, where detection of one picture from a cued condition is sufficient to answer correctly. Secondly, bilateral picture and word presentation will be investigated under conditions where information from both visual hemifields needs to be integrated, i.e. compared at the subcategorical level. For the first condition, a behavioral advantage for bilateral presentation is expected. Presenting the same stimulus to both hemispheres simultaneously often results in faster and better performance than presenting only one stimulus to either hemisphere. This effect has been termed *redundancy gain* or *redundant targets effect* (RTE) and has been found for a variety of different stimuli and across different tasks (e.g. target detection or go/no-go paradigms). Analogous redundancy gains have been found across modalities, for example, when redundant information is presented to the auditory and visual domain (e.g. Schröger & Widmann, 1998), or to the visual and tactile modality (e.g. Forster et al., 2002). Similar evidence that the RTE does not depend on physical identity, comes from studies within the visual modality showing bilateral advantages when semantically equivalent stimuli of different formats are used (e.g. Marks & Hellige, 2003).

The redundant targets effect is much larger in individuals with a section of the corpus callosum (Corballis et al., 2004; Pollmann & Zaidel, 1999; Reuter-Lorenz et al., 1995) or callosal agenesis (e.g. Corballis, 1998). While there was no association between the size of the redundancy gain and type of callosal lesion in one study (i.e. complete callosotomy, commissurotomy, callosal agenesis or anterior callosal sections; Iacoboni et al., 2000), others have indicated that a section of the posterior corpus callosum might be crucial for enhanced redundancy gain to occur (Corballis et al., 2004). Functionally, the absence of visual interhemispheric transfer

because of callosal disconnections appears to be important (Pollmann & Zaidel, 1999).

Different models of interhemispheric interaction have been proposed to explain the RTE, especially for stimulation within the same modality. Three important classes of models can be differentiated by the degree of postulated cooperation during bilateral stimulation: *race models* propose independent processing (e.g. Raab, 1962), *coactivation models* propose additive effects of signal summation (e.g. Miller, 1982), and the *interactive race model* (Mordkoff & Yantis, 1991) assumes specific information exchange.

Race models assume that the two hemispheres operate independently during bilateral trials. Each hemisphere processes the stimulus received from the contralateral visual hemifield. According to this model, responses to redundant stimulation will be on average faster than the mean reaction time to either input alone, because it is always the 'winner' (i.e. faster) of the two competing (i.e. racing) processes that determines the reaction time. However, there is an upper limit on the size of the redundancy gain that can be explained by this model, because reaction time to redundant stimulation cannot be faster than the minimal reaction time to single stimulation. Specifically, according to those models the cumulative distribution functions (CDFs) of reaction latencies to unilateral and bilateral trials have to satisfy the inequality $P(RT < t | S_1 \text{ and } S_2) \leq P(RT < t | S_1) + P(RT < t | S_2)$ (Miller, 1982). Since reaction time distributions sometimes violate this model, alternative models have been developed to explain the RTE: In coactivation models (e.g. Miller, 1982), processing from the two hemispheres converges until a criterion for the decision is achieved. Responses to bilateral trials are faster than to unilateral trials, because the criterion is reached earlier when activations from the right and left hemispheric are

summed up instead of depending on unilateral input only. Under this model, reaction times to bilateral stimulation do not have to obey the inequality equation, because processing effects are thought to be additive not independent.

Coactivation and violation of the race model are not mutually exclusive. Although violations of the race model inequality cannot be explained by race models, but are a sign for coactivation processes instead, the reverse is not true. Coactivation processes can lead to redundancy effects that fall below the limit set by independent race processes (e.g. Pollmann & Zaidel, 1999).

The interactive race model proposed by Yantis and Mordkoff (1991) is an intermediate model, because the two hemispheres do not operate completely independent, but exchange contingency information. In experimental conditions including contingencies (e.g. if a non-target is combined more often with a target than with another non-target), responses to bilateral stimulus presentation can be faster than predicted by the independent race model.

A different neuronal model for redundancy effects which is based on the concept of *transcortical cell assemblies* has been proposed by Pulvermüller and Mohr (1996). This model postulates that by means of associative learning, cortical assemblies emerge that consist of reciprocally connected neurons which represent, for example, concepts, words or images. According to the existence and degree of lateralization for those assemblies, different patterns of hemispheric specialization and hemispheric interaction can be explained. A bilateral (i.e. transcortical) representation is necessary for RTEs to occur, because only then bihemispheric stimulation leads to bihemispheric activation resulting in superior performance. It has been argued that the presence and absence of a redundancy gain for words and pseudowords, respectively, show that previous

learning experience is necessary for bilateral transcortical cell assemblies to develop (Mohr et al., 1994). However, while interhemispheric cooperation was found only for familiar but not for unfamiliar faces, supporting this assumption in some experiments (Mohr et al., 2002; Schweinberger et al., 2003), a redundancy gain was also observed for unfamiliar faces in a different experiment (Compton, 2002). This discrepancy might be explained in part by methodological issues. In the studies, where no redundancy gain was observed for the unfamiliar faces, there was a confound between matching-decision and familiarity. Subjects had to make a yes-no decision whether a face belonged to a famous person or not. Stimuli were familiar (i.e. famous) and unfamiliar faces. Therefore, the familiarity of a face was confounded with a yes-response. Observing a redundancy gain only on match but not mismatch trials might indicate different processing aspects other than differential stimulus representation (Maertens & Pollmann, 2005). Further evidence for a redundancy effect for pictures of unfamiliar faces comes from a same-different identity task. A sample face, which had to be compared to a target face, was split in the middle, so that the left half-face was projected to the right hemisphere and vice versa. The sample face consisted either of two actual half faces or only of a left or a right hemiface, where the second half was a low-contrast half-face stimulus. Performance was best when both halves showed an actual half-face picture, i.e. when both hemispheres directly received stimulus information, compared to unilateral presentation only (Yovel et al., 2003). Thus, a behavioral advantage for bilateral redundant presentation of faces has been observed before and should occur in Experiment 2 as well, but it has not been investigated so far, whether this effect is related to stronger bilateral activation in face-specific visual areas during bilateral stimulation.

3.2.1 Locus of the Redundant Targets Effect

One important question is the stage of processing at which the RTE occurs. While earlier explanatory models were mainly mathematical models and based on abstract concepts (i.e. horse race models first reported by Raab, 1962), more recent models include concepts that correspond to neuronal mechanisms. For example, it has been assumed that coactivation can equal neural summation (e.g. Reuter-Lorenz et al., 1995; Miniussi et al., 1998). Whether neural summation takes place at the perceptual, response decision, or motor level has been investigated by means of behavioral as well as electrophysiological and fMRI methods. However, the locus of the redundant targets effect is likely to be task-dependent and might differ between discrimination and detection tasks, for example.

There is some evidence for an involvement of visual processing in the emergence of a RTE, which would support a correlation between activation in the respective object-selective areas and behavioral redundancy effects: Event-related potentials (ERP) components of extrastriate visual processing showed shorter latencies during bilateral stimulation (Miniussi et al., 1998; de Gelder et al., 2001) and an increase in extrastriate activation was observed during enhanced redundancy in a split-brain patient (Iacoboni et al., 2000). Further evidence suggests that the superior colliculi (SC) play an (additionally) important role for neural summation and RTEs to occur (Corballis, 1998; Savazzi & Marzi, 2004, but see Roser & Corballis, 2002).

On the contrary, it has also been proposed that the RTE arises at later than perceptual processing stages. For instance, results of some behavioral studies implied that the locus of the RTE is at response selection stages (Miller & Reynolds, 2003), or at response preparation and response execution stages (Pollmann & Zaidel,

1999). For example, Giray and Ulrich (1993) found not only faster but also more forceful responses to bilateral targets suggesting motor levels as locus for neural summation effects. However, a subsequent study failed to replicate this effect (Mordkoff et al., 1996). Functional imaging studies found a bilateral increase in activation for bilateral compared to unilateral trials in premotor cortex associated with the RTE, which was also interpreted as evidence for late stages in response preparation as locus for the RTE (Iacoboni & Zaidel, 2003).

Experiment 1 is a category-based target detection task with bilateral picture presentation. Behaviorally, a RTE is likely to occur for both, pictures of faces and pictures of buildings. Unlike in most other paradigms, in Experiment 1 a scrambled picture or a picture of the other category will be presented on unilateral trials. Possible redundancy effects can therefore be compared to unspecific visual stimulation as well as incongruent category information. For the functional locus of possible redundancy effects, related activation differences in the respective object-selective areas will show whether the object-selective areas are involved in the occurrence of this effect.

3.3 Interhemispheric Resource Sharing

Hemispheric interaction has also been investigated on more complex tasks than target detection, for example when information from both hemispheres needs to be integrated and matched on different levels. Performance is often superior on bilateral compared to unilateral trials, e.g. in tasks of letter naming (e.g. Banich & Belger, 1990; Pollmann et al., 2003) or geometrical shape matching (Maertens & Pollmann, 2005). It has been suggested that performing

complex tasks benefits from using resources of both hemispheres when the hemisphere of input reaches its processing limit.

In tasks focussing on hemispheric interactions, stimuli that have to be matched are often presented either in a single visual hemifield alone (within-hemisphere condition) or divided between the visual hemifields, i.e. one in the LVF and one in the RVF (across-hemisphere condition). To avoid confounds with perceptual load, often three stimuli are presented on every trial and a bottom stimulus has to be matched to one of two stimuli presented at the top (Banich & Belger, 1990; Compton, 2002; Koivisto & Revensuo, 2003b). An even more balanced design consists of four simultaneously presented stimuli in an asymmetrical arrangement. The distance of the two top stimuli is enlarged in this displays to account for presumably faster left-to-right scanning than top-to-bottom scanning (Pollmann et al., 2003; Maertens & Pollmann, 2005). In this case, cues indicate the positions of the relevant stimuli for each trial.

Matching decisions are made faster and/or more accurate on across-hemisphere trials than on within-hemisphere trials. However, this bilateral distribution advantage (BDA, Copeland & Zaidel, 1996) occurs only on computational complex tasks (Banich & Belger, 1990, 1990; Weissman & Banich, 2000) or in tasks with lower levels of processing efficiency (Maertens & Pollmann, 2005) provided that the task can be accomplished in both hemispheres. Since additional costs arise for the information transfer between the two hemispheres, on very simple tasks, the opposite advantage for unilateral trials can be observed (Banich & Belger, 1990; Weissman & Banich, 2000). The BDA diminishes in a similar fashion when processing efficiency increases, for instance because of training (Maertens & Pollmann, 2005).

Further support for the assumption that the BDA is indeed based on hemispheric resource sharing comes from functional imaging studies and neural network modeling, where the expected interaction between hemispheric communication and task difficulty was found in the comparison of uni- and bilateral trials in activation differences and modeling parameters. In the fMRI study, the activation patterns of occipital areas related to the visual processing of the letters indicated, that only for the more demanding task, the hemisphere of input reached its resource limit on unilateral trials and activation spread to homologous areas of the other hemisphere (Pollmann et al., 2003). The opposite effect of an increase in activation for bilateral compared to contralateral input was observed for the less demanding letter shape matching task. The same interaction effect between contra- and ipsilateral differences with task difficulty emerged spontaneously in the pattern of processing in the hidden layer of a neural network model representing two fully interconnected 'hemispheres' (Monaghan & Pollmann, 2003). This equivalence of processing pattern and observed effects of activation differences was accompanied by the expected pattern of error rates indicating a BDA for the more complex task only.

A somewhat different explanation for the BDA was suggested by Santhouse et al. (2002). Comparing bilateral with unilateral trials in an fMRI study, the only effect was an increase in activation in dorsolateral prefrontal areas for unilateral trials. The authors argue that this activation reflects additional visual working memory processes carried out during unilateral trials which consequently slow down processing and lead to longer reaction times.

In Experiment 3, a more complex semantic matching task will be used to investigate effects of bilaterally presented words, pictures, and combinations of both. In this task, hemispheric interaction is

necessary, because information from both visual hemifields is required to make the matching decision. There is no within-hemifield condition, because tachistoscopically presenting four pictures and/or words would exceed the subjects' visual capacity, but hemispheric interaction at the across-hemifield condition will be investigated. One of the main questions will be, how the two hemispheres interact during the comparison of words and pictures, because visual word processing is strongly lateralized to the left hemisphere. Different models have been proposed to specifically explain hemispheric interactions under conditions of hemispheric specialization, which will be discussed in the next chapter.

3.4 Hemispheric Specialization and Interaction

The most lateralized function is probably a left-hemispheric dominance for some aspects of language (see Chapter 2.4.2 for lateralization of visual word processing). Evidence comes from early studies on aphasic and split-brain patients (see Toga & Thompson, 2003; Gazzaniga, 2000 for reviews). The degree of lateralization is related to handedness, i.e. right-handers show a more consistent pattern of left-lateralization (Knecht et al., 2000). It has also been suggested that women show less language lateralization than men, i.e. stronger bilateral representation (e.g. Rossell et al., 2002), which might be additionally modulated by the menstrual cycle (Fernandez et al., 2003). However, a recent meta-analysis did not confirm sex differences in language lateralization (Sommer et al., 2004). The underlying mechanisms and the development of this cortical asymmetry are still under debate. Lately, some evidence for a genetically determined influence comes from significant correlations between the supposedly genetically marked scalp hair-whorl

direction, handedness, and the degree of language lateralization (Weber et al., 2005a).

Different cognitive models have been proposed to explain effects of visual hemifield advantages for lateralized presented stimuli in the context of hemispheric interaction patterns. Often, but not always, the well-established behavioral effect of a LVF advantage for lexical processing was investigated regarding different conditions of hemispheric cooperation (see Weems & Reggia, 2004 for a recent review). According to the *callosal relay model*, information that cannot be processed adequately in one hemisphere needs to be 'relayed' across the CC to the more competent hemisphere. According to the *direct access model*, information received in one hemisphere is processed without involvement of the other hemisphere, but different or less efficient strategies might be used in each hemisphere resulting in hemifield advantages. Another model assumes *hemispheric cooperation*, where both hemispheres are involved in task processing either in terms of sharing information (Zaidel & Rayman, 1994), or based on bilaterally distributed stimulus representations (Weems & Reggia, 2004).

One criterion for a direct access mode of processing is a response hand by visual field interaction. If the information is only processed in the hemisphere of input, the hand ipsilateral to the target is always faster than the contralateral hand, because no motor information needs to be crossed. This relative advantage for the right and left response hand results in the interaction effect. The additionally observed main effect of visual hemifield reflects the generally faster response for stimuli presented contralaterally to the specialized hemisphere. If the final stage of processing is always executed in one (e.g. the left) hemisphere, as is assumed in the callosal relay model, the contralateral hand would be faster independent of the

targets' (e.g. words') visual hemifield. Again, the main effect of visual hemifield indicates hemispheric specialization (see Figure 3.1). In callosal relay models, visual hemifield advantages cannot only be interpreted as differences in hemispheric competence, but also as a detrimental effect of callosal transfer, for instance because of slowing effects or information loss. Rather than mutual exclusive patterns of interhemispheric communication, however, those three models may also be seen as extremes on a continuum with dynamic shifts across or even within different task settings (e.g. Zaidel & Rayman, 1994).

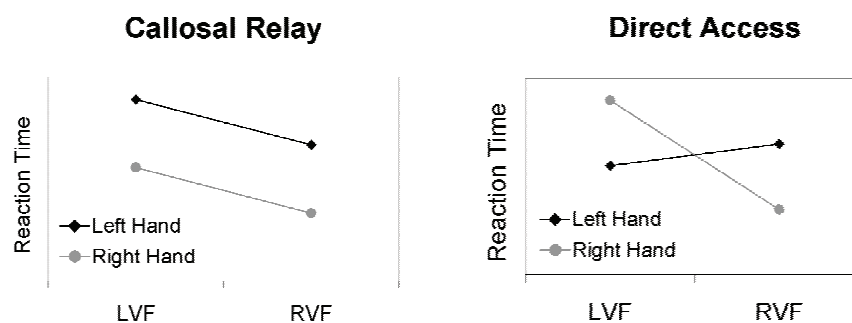


Figure 3.1: *Schematic illustration of direct access and callosal relay. Reaction time patterns to word presentation in the LVF and RVF with left and right responding hands according to the two different models of hemispheric interaction.*

3.5 Bilateral Effect

The above mentioned behavioral advantage for words presented in the RVF has found to be larger when bilateral displays are used instead of unilateral ones (see Boles, 1990 for a review). In those cases, bilateral displays consist of two competing stimuli containing different information and typically spatial cues are used to indicate the relevant target on unilateral trials. This effect of an enhancement of visual field asymmetries, which is also observed on other tasks

than visual word processing, has been termed *bilateral effect*. After ruling out several alternative explanations, Boles (1990) proposed that the bilateral effect is due to homologous activation during bilateral stimulation which disrupts communication between the hemispheres. Because of this disruption in communication, interhemispheric interaction supposedly shifts from cooperative to more independent processing on bilateral trials. Consistent with this increase in independent processing on bilateral trials, in a behavioral study, a significant hand by visual field interaction was only observed for uni- but not for bilateral trials, i.e. suggesting direct access processing only during unilateral stimulation (Iacoboni & Zaidel, 1996). Additionally, error rates and decision latencies were increased in bilateral trials, which was interpreted as evidence that interhemispheric cooperation during unilateral trials is beneficial, particularly for the less competent right hemisphere. In contrast, Olk & Hartje (2001) did not find a visual field by response hand interaction for bilateral trials. They only observed a general RVF advantage along with the bilateral effect. The absence of the interaction effect was interpreted as supporting evidence for the callosal relay model and the bilateral effect was interpreted as interhemispheric competition. Based on the assumption of callosal relay during bilateral stimulation, all information is presumably processed in the specialized left hemisphere. In bilateral, but not in unilateral trials, information from the LVF competes with the information from the RVF in the left hemisphere which has the advantage of being directly projected from the contralateral field. This negative competition effect leads to an increase in reaction times for stimuli in the LVF and therefore to an increase in visual field differences. While the reason for the different results obtained in both experiments is unclear, the increase in reaction time for

bilateral trials observed consistently in both experiments shows that a simultaneously presented word in the opposite visual field affects processing even when this stimulus is irrelevant. Similar interference effects have been reported with other stimulus formats as well (e.g. Levy et al., 2003, Marks & Hellige, 1999).

In Experiment 1, congruent, incongruent and unspecific categorical visual information will be presented in the opposite visual hemifield. Based on the above-mentioned findings, an influence of this stimulation difference should be observed, although the experimental paradigm does not include spatial cueing of relevant and irrelevant information. Possible effects of a left visual field advantage for face detection might therefore be enhanced analogous to the bilateral effect in word processing.

In Experiment 2, the effects of hemispheric specialization for visual word processing will be investigated in a semantic matching task of pictures and words. The analysis of behavioral and functional imaging data will indicate the theoretical model that best describes the observed pattern of interhemispheric interaction in this task.

3.6 Hemispheric Control

Apart from the question which hemisphere might be more specialized in processing stimuli of certain kinds, there is also the question of hemispheric control. The concept of *metacontrol* refers to the mechanisms that determine which hemisphere dominates processing during bilateral trials, i.e. when both hemispheres have access to the same stimulus information. A dissociation between hemispheric competence and hemispheric control was first found in the study of split-brain patients. The more competent hemisphere was not necessarily the hemisphere in control (Levy & Trevarthen, 1976). This finding has been extended to interactions in the intact

brain (e.g. Hellige, 1990; Urgesi et al., 2005). For example, in same-different matching task for pictures of faces, two successively presented drawings of faces were either identical or different in one feature (e.g. hair, eyes, etc.). The first picture was always presented centrally, the second in LVF or RVF or to both visual hemifields simultaneously (bilateral, BIL). Comparing BIL trials with LVF and RVF trials, the pattern of reaction times for the correct detection of each feature was identical for BIL and RVF-trials, but different for BIL and LVF-trials. Reaction times for RVF- and LVF-trials varied across different features without a general visual hemifield advantage. The comparable pattern of reaction time data for RVF and BIL trials was taken as evidence for metacontrol of the left hemisphere. That the pattern for BIL trials was generally comparable to RVF trials, i.e. even for feature conditions where faster reactions were on average given for LVF trials, was taken as evidence that the dominating hemisphere is not necessarily the more competent (Hellige et al., 1988).

In healthy individuals, patterns of hemispheric control can be assessed in different ways. Firstly, the hemisphere in control can be inferred by the interaction of an independent variable *V* with performance in LVF and RVF trials. If the influence of the independent variable *V* on performance in bilateral trials is similar to one (and only one) of the unilateral conditions, it can be inferred that bilateral processing is controlled by the respective hemisphere (Zaidel & Rayman, 1994). For example, in a study by Hellige and Michimata (1989), reaction times were assessed in LVF, RVF and BIL trials in one experimental paradigm under two different task demands (categorical and coordinate spatial judgments). The difference in reaction time between the two instructions was similar for RVF and BIL trials, but dissimilar for LVF and BIL trials. This was

interpreted as dominance for the LH processing mode in BIL trials. Secondly, hemispheric control can be inferred if differences in hemispheric processing strategies are evident in performance during LVF and RVF trials. Performance in bilateral trials can then be compared to both trials, and similarity to either LVF or RVF trials indicate which hemisphere controls the process on BIL trials (Hellige et al., 1988; Luh & Levy, 1995). If performance in bilateral trials resembles performance in neither of the unilateral trial conditions, however, behavioral patterns are difficult to explain within the concept of metacontrol (Banich & Karol, 1992). However, large individual differences or variations across trials in the distribution of hemispheric control might account for some of the inconsistent results (Luh & Levy, 1995).

With respect to a possible cortical location of control processes related to hemispheric specialization, a recent fMRI study found that the anterior cingulate cortex was involved in hemispheric control processes on a lateralized task (Stephan et al., 2003). Using identical perceptual stimulation, this area was coupled more strongly to left-hemispheric cortical areas during a language-specific task and more strongly to right-hemispheric cortical areas during a visuo-spatial task. Activation of the anterior cingulate cortex was also observed in a letter-matching task during conditions of interhemispheric transfer (Pollmann et al., 2003).

3.7 Summary and Implications for Present

Experiments

The last chapter discussed patterns and models of interhemispheric interaction, ranging from specific information transfer across the hemispheres to complex patterns of interhemispheric cooperation. The fMRI experiments of this dissertation investigate effects of

lateralization and specialization especially at the level of higher visual analysis carried out in object- and stimulus-specific areas, respectively. Along with hemispheric differences in activation, patterns of interaction based on behavioral and functional imaging data will be examined.

In the category detection task of the first experiment, the bilateral presentation of pictures of faces and buildings should speed up the responses compared to only unilateral presentation or compared to incongruent category information in the opposite visual hemifield. Furthermore, it will be investigated whether this effect depends on presentation of the identical stimuli in both visual hemifields, or whether it is independent of physical identity and extends to two different exemplars from the same category. Along with these expected behavioral results, activation differences in the respective object-selective areas indicate whether these high-level visual processing stages are involved in the occurrence of a possible RTE or whether the locus of this effect occurs at different processing stages. The use of bilateral displays during this experiment could further enhance a possible right visual field advantage for face processing.

In the third experiment, hemispheric interaction will be investigated, especially under conditions of hemispheric specialization. Since the left hemisphere is supposedly specialized in visual word form processing, a behavioral advantage for words directly presented in the contralateral field is expected. The analysis of activation differences and response patterns allows for an evaluation of the different theoretical models of hemispheric interaction to determine which model can best account for the observed results.

With respect to differences in hemispheric control, an analysis of reaction times from uni- and bilateral trials can be used to investigate whether responses to bilateral trials resemble either LVF or RVF trials. For example, if reaction times in bilateral as well as in LVF trials are similar and generally faster than reaction times in RVF trials, hemispheric control of the right hemisphere during bilateral trials could be inferred. However, control of one hemisphere does not imply an exclusive or a more efficient processing of the relevant stimuli in the respective hemisphere. For the semantic matching, hemispheric control differences are possible for words presented ipsi- and contralaterally to the specialized hemisphere. In this case, activation differences in regions of the anterior cingulate cortex could be an indicator for hemispheric control processes or interhemispheric transfer of information (Pollmann et al., 2003; Stephan et al., 2003).

4 Methods

4.1 Overview of Methods in the Field

Effects of lateralization and hemispheric interactions in humans have been approached by various methods. An non exhaustive list includes patient studies, behavioral and functional imaging experiments (e.g. PET, fMRI, MEG, ERP studies), as well as neural network modeling. As mentioned above, if damages or deafferentation of specific cortical regions result in a specific deficit, it can be suggested that the impaired function is related to these cortical areas. Split-brain patients can be seen as a special case of deafferentation (i.e. almost completely from all contralateral areas), and they have been intensively studied to determine effects of hemispheric lateralization and (the absence of) hemispheric interaction (see Gazzaniga, 2000 for a review). For many other patients, however, the degree of deafferentation and functional disruption can often not be determined exactly. Another group of patients showing a reduced amount of interhemispheric interaction are patients suffering from multiple sclerosis, because the CC is specifically affected by the demyelination (Banich, 1998). Other research approaches in the field of hemispheric interaction include correlations of behavioral effects to anatomical brain differences (e.g. Hellige et al., 1998), and the influence of factors like gender, handedness, menstrual cycle, etc. on patterns of interhemispheric

interaction and cerebral asymmetries (e.g. Luders et al., 2003), along with life-span investigations to assess relations to child development and aging.

Another classical paradigm, that is used to assess hemispheric differences and interactions in the auditory domain is the *dichotic listening task*. In this paradigm, similar but slightly different stimuli are presented simultaneously to the left and right ear. Lateralization effects, which can be interpreted as differences in hemispheric processing efficiency, become evident in advantages for the left or right ear. For example, a right ear advantage (REA) for the identification of verbal stimuli is often observed, which is line with a left-hemispheric lateralization of some language-related processing (see Bryden & Bulman-Fleming, 1994 for a review). Similarly to behavioral studies in the visual domain, patients with lesions disturbing transfer of auditory information across the CC show a more pronounced disadvantage for stimuli presented to the left ear (e.g. Pollmann et al., 2002).

A different approach to investigate patterns of hemispheric interaction is based on neural network modeling. Founded on cognitive models, behavioral effects can be simulated with artificial neural networks. If data obtained from actual measurements of specific tasks fit well to specifically trained neural networks, the underlying parameters might be comparable and indicate a possible realization of behavioral effects at the neuronal level (e.g. Monaghan & Pollmann, 2003; Weems & Reggia, 2004).

4.2 Divided Visual Field Technique

The most commonly used paradigm to investigate effects of interhemispheric specialization and interaction in the visual domain in healthy subjects is the divided visual field technique (see Bryden

& Bulman-Fleming, 1994 for a review). Taking advantage of the anatomical characteristics of the human visual system, where information from the LVF is initially routed to the right hemisphere (RH) and vice versa (RVF-LH), each hemisphere can be stimulated separately by tachistoscopic presentation of stimuli in the contralateral hemifield. The question as to whether the two visual hemifields overlap at the vertical meridian is still under debate. Some evidence suggested a bihemispheric representation of the fovea, others have favored a split-fovea model without overlapping foveal representation (see Brysbaert, 1996 for a review). Generally, the two hemispheres are connected via the cerebral commissures, i.e. the lateralized presented information is ultimately available to both hemispheres.

Differences in accuracy or reaction times between LVF and RVF conditions in the divided visual field technique paradigm have been interpreted as differences in processing proficiency for certain tasks or stimuli between the hemispheres, i.e. like the RVF advantage in the lateralized lexical decision tasks. To examine effects of interhemispheric transfer and/or interaction, unilateral conditions were compared to conditions where both hemispheres are stimulated. As already described in the section of different models for interhemispheric interaction, different patterns of interhemispheric communication can not only be assessed through differences in mean reaction time or differences in mean accuracy for uni- and bilateral trials, but also in the investigation of interaction patterns, e.g. with respect to VF and response hand effects. While historically the divided visual field study was a major breakthrough for the non-invasive investigation of laterality effects, there are some problems associated with this technique as well. Difficulties and potential nuisance variables that have to be controlled for include the

need for strict fixation and possible confounding variables as order of report or disproportional attentional allocation (e.g. Young & Ellis, 1983). In the fMRI experiments of this dissertation, for example, eye movements will be especially monitored with a video camera (see method sections for details).

4.3 Functional Magnetic Resonance Imaging

Magnetic resonance imaging (MRI) has been used for many years to obtain structural images of human anatomy and tissue structure. It is founded on the principles of Nuclear Magnetic Resonance (NMR). NMR is based on an intrinsic property of all atomic nuclei: the nuclear spin. Because of this inherent rotation, the electrons of the nucleus generate a magnetic field, i.e. each nucleus has a magnetic dipole moment (MDM) parallel to its rotation axis. For human NMR and fMRI, hydrogen atoms are the most important, because they are the most common in the human body. During NMR, a strong static magnetic field is applied which influences the general population of hydrogen nuclei. Each nucleus will align either parallel or anti-parallel to the external magnetic field and this alignment is equivalent to states of low and high energy, respectively. The number of molecules in the low-energy state, i.e. the number of molecules aligned parallel to the external magnetic field, will be slightly larger than the number of molecules in the high-energy state. Although this numerical difference is tiny, it can account for the observed NMR signal changes. The larger number of parallel aligned molecules, results in the formation of a net magnetization (M) also parallel to the applied magnetic field. Furthermore, the MDM will precess around the direction of the main magnetic field with a specific Larmor frequency. This frequency is linearly correlated to the strength of the applied magnetic field and specific

for different atoms, i.e. the Larmor frequency can be determined for hydrogen atoms at different field strengths.

Next, an oscillating electric field with the same Larmor frequency (usually at a frequency of several MHz) is applied perpendicular to the first static magnetic field. The spins absorb energy (i.e. they resonate), leading to a tipping of M into the traverse plane (i.e. in the direction of the applied oscillating field). After the oscillating magnetic field is turned off, the magnetization returns to the previous state of alignment along the static magnetic field. The nuclei relax, i.e. they release the energy absorbed to return to the specific state of balance again in the form of a wave with the Larmor frequency. This transmission is the source of the MRI signal.

The time taken for the protons to relax can be described by two independent parameters. The first (T_1) is termed longitudinal relaxation and refers to the time taken for the magnetic vector M to return to its resting state. The second (T_2) is termed transverse relaxation time and refers to the time duration until the spinning protons lose the phase coherence with the nuclei spinning perpendicular to the main field. Since this effect is mainly due to interactions between spins, it is also been called spin-spin interaction. A faster relaxation time, where the loss of common phase includes both spin-spin interactions and magnetic field inhomogeneity is a time constant called T_2^* . This parameter is especially important for the fMRI BOLD used in the current experiments.

Functional Magnetic Resonance Imaging is a recently developed neuroimaging technique. Its main advantages are its non-invasiveness, along with a high spatial resolution and a temporal resolution satisfactory for most tasks. FMRI does not measure neuronal activity directly, instead changes in activation are assessed

via the associated vascular response, i.e. mostly differences in blood oxygenation. Although the precise relationship between the fMRI signal and neural activity is still unclear, neural activity is closely related to transient changes in regional blood flow. This is based on the increase in metabolism during neuronal activation, which requires additional oxygen because of the enhanced oxygen consumption (see Jueptner & Weiller, 1995 for a review). This tight relation between blood flow and metabolic rate has been termed neurovascular coupling.

BOLD-Effect

The fMRI BOLD-signal relies on the different magnetic properties of blood with high and low levels of oxygenation. The haemoglobin molecule is the oxygen carrier in blood. Oxygenated and deoxygenated haemoglobin have different magnetic properties. Deoxyhaemoglobin is paramagnetic, whereas oxyhaemoglobin is diamagnetic. The presence of the paramagnetic deoxygenated haemoglobin causes local distortions in the magnetic field leading to susceptibility differences between the vessel containing the blood and its surrounding tissue. Such susceptibility differences cause faster dephasing of the NMR proton signal, i.e. a faster T_2^* relaxation leading to a signal decrease in T_2^* -weighted images. An increase of deoxygenated blood is related to a signal decrease. However, under stimulation mostly increases in fMRI signal are observed, indicating a decrease in deoxyhaemoglobin. This rather counterintuitive increase in the proportion of oxygenated haemoglobin during neural activity is based on a complex pattern of physiological effects with changes in cerebral blood flow and cerebral blood volume. Generally, the increase in the cerebral blood flow is much larger than the amount of oxygen that is consumed,

leading to an overall increase in the ratio of oxyhaemoglobin to deoxyhaemoglobin and therefore to signal increases.

The exact relation between BOLD signal changes and activation processes at the cellular level is still investigated, although an increase in signal appears to be roughly positively correlated with neuronal activation (see Nair, 2005 for a recent review). However, Logothetis et al., (2003) found that the BOLD signal was most strongly related to the local field potentials, i.e. representing synaptic input rather than activation spikes.

Temporal characteristics of the BOLD signal to brief episodes of neural activity, the hemodynamic response function, have been estimated and appear to be relatively constant, e.g. across different trials (Aguirre et al., 1998b). Generally, the signal begins to rise soon after stimulus presentation and reaches its peak around 4 to 6 seconds after onset of stimulus presentation. After a period of about 5s to 12s it returns to baseline level.

4.3.1 Invariant fMRI Procedures

While some of the parameters were adapted for each experiment, the following technical details remained constant across the experiments in this dissertation.

Functional images were collected at 3T by a Bruker 30/100 Medspec system (Bruker Medizintechnik, Ettlingen, Germany) equipped with the standard bird cage head coil, using a gradient echo EPI sequence ($TR = 2000$ ms, $TE = 30$ ms, flip angle = 90°). Twenty-four axial slices were acquired parallel to the AC-PC plane, allowing for whole brain coverage. Slice thickness was 4 mm and interslice distance 1 mm, with a 19.2-cm FOV and a 64 x 64 image

matrix. In some subjects the FOV was adapted to accommodate for their large heads (see method section of each experiment).

Subjects were lying backward on the scanner bed and foam padding was used to reduce head motion. Stimuli were presented through LCD goggles (VisuaStim XGA, Resonance Technology), with a virtual distance of 120 cm distance.

4.3.2 Invariant Analysis of Functional Imaging Data

All functional data collected in this dissertation were analyzed using the LIPSIA software package (Lohmann et al., 2001). While some of the parameters were also adjusted for each experiment due to differences in experimental paradigms (e.g. based on the average difference between critical trials), some steps of functional analyzing were the same across the three experiments. In detail, slice acquisition time differences were corrected by sinc interpolation. Movement artifacts were corrected using a matching metric based on linear correlation. All functional data sets were individually registered into a 3D-stereotactic coordinate system using subjects' individual high resolution anatomical images obtained in a previous scanning session. The 2D-anatomical slices, geometrically aligned with the functional slices, were used to compute a transformation matrix, containing rotational and translational parameters, that register the anatomical slices with the 3D reference T1-data set. Geometrical distortions of the EPI-T1 images were corrected using additional EPI-T1 refinement on the transformation matrices. These transformation matrices were normalized to the standard Talairach brain size (Talairach & Tournoux, 1988) by linear scaling, and then finally applied to the individual functional data. The normalized 3D-datasets had an isomorphic voxel size of 3mm side length. The statistical evaluation was based on the general linear model for

serially autocorrelated observations (Friston et al., 1995 and Worsley & Friston, 1995). For each individual subject statistical parametric maps (SPM) were generated. The design matrix for event-related analysis was created using a synthetic model of the hemodynamic response function and its temporal derivative (Josephs & Henson, 1999). The model includes an estimate of temporal autocorrelation. The effective degrees of freedom were estimated as described by Worsley and Friston (1995).

A random effects analysis was calculated (Holmes & Friston, 1998) by computing one-sample t-tests of contrast-maps across subjects. Data were analyzed using the general linear model (Friston et al., 1995). Event-related analyses were performed using a model of the hemodynamic response and its temporal derivative (Friston et al., 1995; Josephs & Henson, 1999). Group activation was calculated using a random-effects model (Holmes & Friston, 1998).

5 Experiment 1

5.1 Introduction

The first experiment investigated the influence of input from the opposite visual hemifield on behavioral measures and on activation of category-selective areas in a category-detection task. In an event-related fMRI study using the divided visual field paradigm and a match-to-sample task, both hemispheres were stimulated simultaneously with two pictures, and effects of different stimulus combination on performance and on the BOLD effect were examined.

Main effects of visual hemifield on detection were not expected for pictures of buildings based on the overall absence of visual field advantages on object detection (Biederman & Cooper, 1991; but see Kovisto & Revonsuo, 2003b; see Chapter 2.4.1). To my knowledge, there are no experiments specifically investigating visual hemifield differences on building detection.

For faces a LVF advantage could be noticeable (Dutta & Mandal, 2002; Levine et al., 1988; McCarthy et al., 1999; Rizzolatti et al., 1971; Young et al., 1985). This could be the case, especially because the bilateral stimulation in this experiment could promote a bilateral effect. The observation of a LVF, however, is not inevitable. Numerous other studies have also failed to demonstrate hemifield differences (Basu & Mandal, 2004; Kampf et al. 2002, 2005; Mohr et al., 1996).

Concerning lateralization effects in terms of hemispheric activation differences, a stronger response in the right hemisphere could be observed for pictures of faces (e.g. Kanwisher et al., 1997; Hasson et al., 2002; Druzgal & D'Esposito; 2003; Puce et al., 1996; Sergent et al., 1992, but see Halgren et al., 1999; Peelen & Downing, 2005; see Chapter 2.4.1). No lateralization effects are expected for PPA activation. Effects of the visual hemifield on activation differences in the PPAs are rarely reported and I am not aware of studies specifically investigating this effect. Even though pictures were presented lateralized and not foveally, bilateral activations for the PPA should still be observed. A higher responsiveness towards peripheral stimulation could lead to a general enhancement of PPA activation, but could not account for effects of the different conditions of picture presentation of buildings, because all pictures were presented with the same distance from the center (Levy et al., 2004).

Behaviorally, a beneficial effect for presenting two stimuli from the same category could be expected indicating the RTE (see Chapter 3.2). In contrast to the paradigm used in this experiment, however, in paradigms demonstrating the effects often single stimuli are presented alone in the LVF or RVF in unilateral trials. In this paradigm, in trials with only one relevant stimulus in the LVF or RVF, unspecific or incongruent category information will be presented in the opposite visual hemifield.

5.2 Materials and Methods

5.2.1 Participants

Fourteen volunteers participated in this study (7 males). The data of one subject was excluded because of measurement artifacts. All

subjects were consistent right handers according to their score in the Edinburgh Handedness Inventory (Oldfield, 1971). Subjects' age was in the range of 20 to 29 years, with a mean age of 25 years. All subjects were native speakers of German and had no history of neurological or psychiatric disease. All subjects gave informed written consent according to the guidelines of the Max-Planck-Institute. The fMRI-procedures were approved by the University of Leipzig ethics committee.

5.2.2 Stimuli and Procedures

The experimental stimuli consisted of 30 color photographs which were presented on a grey screen. For the building category, the pictures showed 15 different types of buildings; for the face category, the pictures showed 15 different human faces (see Appendix for a list of stimuli). All faces were depicted in frontal view with about the same amount of hair and background visible. Scrambled versions of all picture and word stimuli were generated using Fourier transformations on red, green, and blue components that left the spatial frequencies the picture intact (<http://www.princeton.edu/~mpinsk/science.htm>).

All scans were performed in a single session with an absolute scanning time of about 45 minutes. A fixation cross was visible throughout the entire experimental block. The task was a delayed matching to sample task. At the beginning of each mini-block, subjects were presented with a sample picture for 200ms that showed either a building or a face indicating the target category for the five following trials. During each trial, two pictures were presented simultaneously for 200ms in the left and right visual hemifield. Subjects had to decide as quickly and accurately as possible whether at least one picture belonged to the target

category. The picture identical to the sample picture was never shown during matching trials of one block (see Figure 5.1).

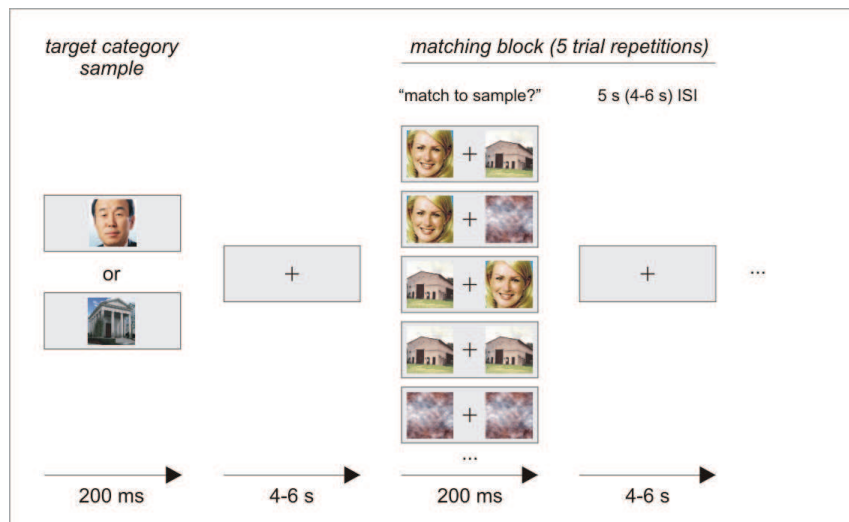


Figure 5.1 *Experimental paradigm of experiment 1. At the beginning of each mini-block a picture was presented for 200ms indicating the relevant category (i.e. face or building). This was followed by five trials with simultaneous presentation of two stimuli, one in each visual hemifield. Within each trial, participants had to decide as quickly as possible whether at least one of the stimuli belonged to the relevant category.*

For face-face and building-building combinations, the contralateral stimulus could either be the identical or a different exemplar. Additionally, during null-event trials no pictures were presented, but the fixation cross remained on the screen. The order of the conditions was pseudorandomized, such that the transition probabilities were as balanced as possible and each condition occurred equally often at the positions one to five. The identical condition was never repeated twice. By rotating conditions, four different sequences of the experimental phase were obtained that were balanced between subjects

The time lag preceding and following each condition where only the fixation cross remained visible was either four, five or six seconds to reduce the overlap of the BOLD-responses elicited by critical trials. In a previous study, it was demonstrated that blood-oxygenation-level-dependent (BOLD) signal changes related to the critical trials obtained in this way are as large as the difference between critical and baseline trials presented in isolation (Pollmann et al., 2000).

The response hand was varied during the course of an experiment following an A-B-B-A scheme. Half of the subjects began with the right and half with the left hand. Subjects indicated match trials by pressing the index finger and pressing the middle finger for mismatch trials for the left and right hand, respectively.

5.2.3 FMRI Procedure

Baseline drifts were corrected by high-pass filtering, implemented using a discrete Fourier transform with a cut-off period of 55s. In the spatial domain, the data were filtered using a Gaussian filter with FWHM = 7 mm.

The respective areas of object-selective processing, i.e. FFA and PPA, were defined as a priori ROIs and voxels in these with a Z score greater than 3.09 ($p < 0.001$ uncorrected) were considered. All voxels outside these regions were significant at $p < 0.0001$ uncorrected ($Z > 3.72$).

5.3 Results

5.3.1 Behavioral Results

Trials with reaction times above or below three standard deviations of individual means calculated for sample-building and sample-face

trials separately were excluded from the analyses. For the reaction time data, only correctly answered trials were considered.

Effects of contralateral stimulation on reaction time and accuracy were analysed separately for each category. First, it was tested whether the conditions of bilateral stimulation with two pictures of the same category and two identical pictures differed. This was not the case, neither for buildings nor for faces in both behavioral measures (all $p > 0.05$). Therefore, trials were collapsed to one redundant condition for each category.

Testing for visual field effects, MANOVAs were calculated with the factors Visual Hemifield (LVF, RVF) and Contralateral Stimulation (scrambled, other category) in match trials for buildings and faces for the reaction time and accuracy data, respectively. There were no interaction effects between the two factors for either category and no main effect for Visual Field, so that trials were collapsed across both visual field conditions to one scrambled and one other-category condition for faces and buildings.

To determine effects of contralateral stimulation, MANOVAs were calculated with the factor Condition (redundant, scrambled, other category), in matching trials for both categories. For the reaction time data, there was a main effect of Condition for buildings [$F_{(1,12)}=11.03$; $p < 0.05$] as well as for faces [$F_{(1,12)}=5.1$; $p < 0.05$]. Post-hoc T-Tests revealed that the only significant difference after stepwise Bonferroni correction (Holm, 1979) was a faster reaction to redundant stimulation than to combinations with a picture from the other category. This was true for faces [$T_{12}=3.26$; $p < 0.05$] as well as for buildings [$T_{12}=5.06$; $p < 0.05$; see Figure 5.2].

For the accuracy data, there was a main effect of Condition only for buildings [$F_{(1,12)}=11$; $p < 0.05$] driven by a higher accuracy rate for

redundant stimulation in comparison to combinations with scrambled pictures in the contralateral field [$T_{12}=4.06$; $p<0.05$; corrected for multiple comparisons (Holm, 1979)]. As can be seen in Figure 5.2 the effect of faster reactions to redundant than mixed building-face conditions cannot be explained by speed-accuracy-trade-off effects, since the same trend is observed in the accuracy rate for buildings and no difference is observed in the accuracy for faces.

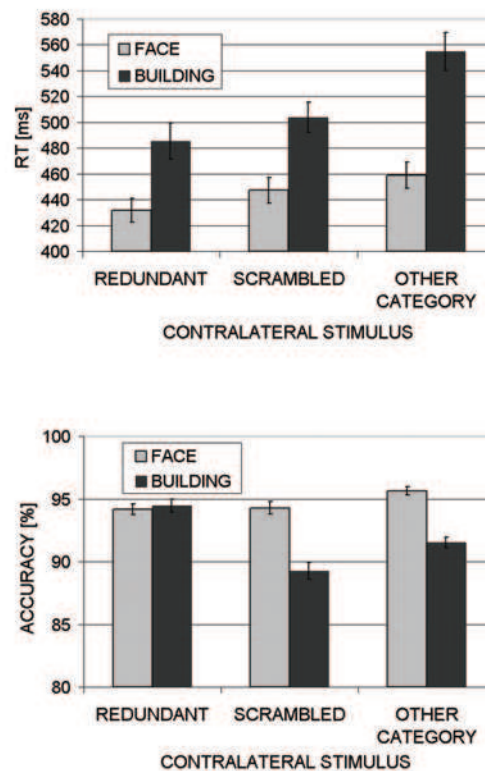


Figure 5.2 Behavioral results of Experiment 1. Reaction times are averaged across visual hemifields, only correct answers to match trials were considered. Lighter grey bars represent face-trials and black bars indicate building-trials. Error bars indicate the standard errors of the means.

5.3.2 Imaging Results

Contrasting bilateral presentation of pictures of faces against bilateral presentation of pictures of buildings, the relevant object-selective areas could be identified. For pictures of faces, FFA activation was restricted to the right hemisphere. Stronger responses to bilateral face than picture presentation was right-lateralized at $37x -56y -11z$ (FFA). Peaks of activation for the PPAs were obtained bilaterally at the expected locations of $-26x -44y 9z$ (LH PPA) and $25x -44y -9z$ (RH PPA).

Based on the behavioral results of faster reactions to bilateral redundant stimulation than to mixed face-building conditions, the corresponding contrasts were calculated for matching trials of each category; i.e. [(same category + same category/identical picture) – (face-building + building-face)]. In both contrasts, bilateral redundant stimulation lead to higher activation in the respective object-selective area than to mixed stimulation (Fig. 5.3). For faces, a peak of activation was found at $40x -59y -3z$; for buildings, peaks of activation were located at $-29x -42y -3z$ and $28x -47y -6z$. Additional activation ($p < 0.0001$) for the mixed condition was found for the building contrast in the median wall, especially at the cingulate sulcus ($4x 34y 29z$) and the precuneus $-2x -62y 44z$.

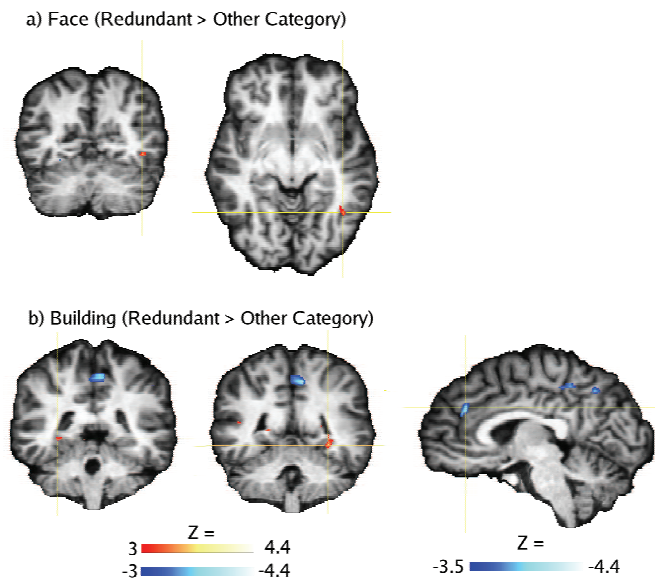


Figure 5.3 Group images averaged across match trials separately for each category. Colorscales indicate z-scores. The red scale indicates stronger responses to redundant trials, the blueish scale indicates stronger responses to mixed building-face trials. In the contrast of mixed building-face trials with bilateral redundant trials, an increase in the object-selective areas was found a) Stronger activation for redundant stimulation with two pictures of faces compared to building-face combinations was found in the FFA b) Stronger activation for redundant stimulation with two pictures of buildings compared to building-face combinations was found in the left and right hemispheric PPA. Additionally, stronger activation in the cingulate cortex and precuneus was found for the mixed face-building condition.

Comparing match trials of bilateral redundant with match trials of scrambled combinations, there were no significant differences at the location of the PPAs for the pictures of buildings, but stronger activation for pictures of faces at 37x -57y -9z; i.e. at the location for the FFA. For picture of buildings, there was a significant ($p < 0.0001$) activation at the cuneus near the parieto-occipital gyrus at 10x -65y 17z. No other activation peaks were obtained at this threshold for the pictures of faces (Fig 5.4).

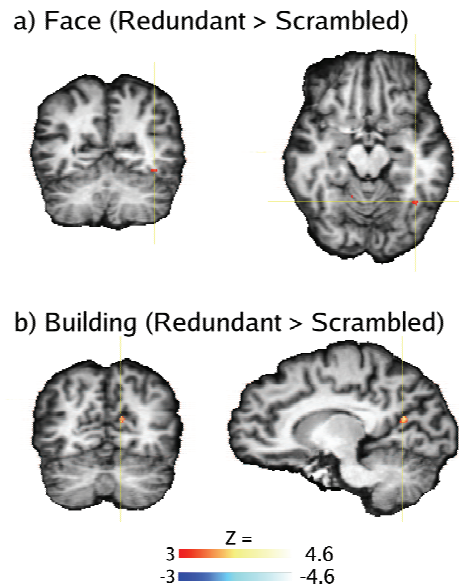


Figure 5.4 Group images averaged only across match trials. Colorscales indicate z-scores, the red scale indicates stronger responses to redundant trials, the blueish scale indicates stronger responses to combinations of the preferred picture with scrambled pictures. a) Stronger activation for redundant stimulation with two pictures of faces compared to scrambled-face combinations was found in the FFA b) Stronger activation for redundant stimulation with two pictures of buildings compared to building-face combinations was found in the cuneus near the parieto-occipital sulcus.

Comparing match trials of combinations with scrambled pictures to combinations with pictures from the other category; there were no significant activations at the location of the PPAs and FFAs. However, there was a trend for higher activation in the PPAs for combinations with scrambled compared to combinations with faces ($p < 0.005$ Fig 5.5).

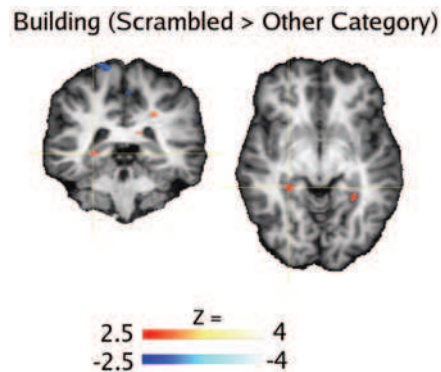


Figure 5.5 *Stronger activation to combinations with scrambled pictures compared to combinations with faces was found for pictures of buildings and the PPAs bilaterally.*

5.4 Discussion

There was no main effect of visual hemifield in the behavioral data, neither for the detection of faces nor for the detection of buildings. Even though the category-specific activation in occipito-temporal cortex was clearly right-lateralized for pictures of faces, there was no significant advantage for the detection of faces presented in the contralateral (i.e. left) visual hemifield. A direct correlation between face detection and lateralization of face-related activation has rarely been investigated. In an ERP study, a LVF advantage for face processing was generally associated with a lateralized N170 component, but there was no correlation between behavioral measures and the amplitudes of the ERP components (Yovel et al., 2003, but see mentioning of unpublished data). Overall, these results again indicate that the LVF advantage for faces is not a robust phenomenon, but appears to strongly rely on specific task or stimulus characteristics, of which the exact neural correlates need to be investigated further (see Sergent, 1995 for a review).

There were three types of stimulus combinations for each category that were compared in their effects on behavioral and activation differences in their respective object-selective area: scrambled, other category (i.e. mixed building-face combinations), and redundant (i.e. identical picture or picture of the same category) combinations.

The behavioral results showed an advantage for redundant over mixed combinations, i.e. category-based matching decisions were made faster when a picture from the same category was presented in the opposite visual hemifield as opposed to a picture from the other category. Faster reaction times to redundant than to mixed combinations was associated with an increase of activation in the respective object-selective areas. This was true for both categories, i.e. for pictures of faces and FFA activation as well as for pictures of buildings and PPA activation. Whether this difference in performance and object-selective activation was primarily based on a relative increase during bilateral stimulation, i.e. a neural summation effect for bilateral redundant conditions (e.g. Minussi et al., 1998), or based on a relative decrease in activation for conditions of incongruent category information, i.e. for competing categorical information (e.g. Fink et al., 2000; but see Schwartz et al., 2004) cannot be established unequivocally, because the comparisons against the scrambled conditions yielded mixed results and differed between the two categories.

On the one hand, if the effect was primarily due to reduced activation for mixed combinations, due to interference-like effects at the category-level, responses to scrambled combinations should be stronger than to mixed combinations as well. There were no significant activation differences in the contrast of scrambled combinations to mixed combinations for the preferred pictures in the

FFA and PPAs. However, the trend of higher PPA activation in trials with pictures of buildings combined with scrambled pictures as compared to trials with pictures of buildings combined with pictures of faces support a relative decrease in PPA activation during presentation of incongruent information.

On the other hand, if the effect was primarily based on stronger activation to redundant stimulation than to unilateral stimulation, higher activation should be observed in the same way for redundant stimulation conditions if these conditions were contrasted to scrambled combinations. The corresponding contrasts, however, showed mixed results. There were no activation differences in the PPAs for the redundant against the scrambled combination. Instead, higher activation for two pictures of buildings compared to one picture in combination with a scrambled picture was observed near the parieto-occipital gyrus. The functionality of this activation for the current task is uncertain. Similar activation has been found in other visual tasks, for example during perception of visual images and scenes (Stiers et al., 2005) and during visual search tasks (Makino et al., 2004). Behaviorally, no difference in reaction time was observed, but responses were more accurate for bilateral stimulation than for combinations with scrambled pictures. For faces, stronger activation for bilateral redundant pictures as compared to combinations of faces with scrambled pictures was observed at the right-hemispheric FFA, although no significant behavioral effect was obtained.

Taken together, there was a correspondence between behavioral and activation differences for the mixed against the redundant comparison: Faster decision latencies for stimulation with two pictures from the same category instead of one picture from each category was associated with stronger activation in the respective

object-selective areas. A redundancy effect for familiar but not unfamiliar faces has been reported before (Mohr et al., 2002; Schweinberger et al., 2003). It has been suggested that only familiar faces are presented in bilateral cell assemblies (Pulvermüller & Mohr 1996) and that bilateral neuronal representation is necessary for redundancy gains to occur (see Chapter 3.2). In this experiment, pictures of unfamiliar faces were shown, and a redundancy gain for unfamiliar faces was also observed in other experiments (Compton, 2002). Along with the right-lateralized activation for pictures of faces during both, uni- and bilateral stimulation, the cell-assembly theory cannot account easily for the obtained redundancy effect.

Instead, the relation between increased activation and faster responses could indicate that neural summation effects in the object-selective areas are responsible for the faster reaction times. Even though object-selective areas are supposedly non-retinotopic and are activated by contra- as well as ipsilateral input, it is plausible that information from both visual hemifields contribute to the activation, i.e. activation increases when the object-selective areas obtain category-information from the contra- *and* ipsilateral visual hemifield, instead of input from the contra- *or* the ipsilateral visual hemifield. Alternatively, a part of the effect could also be explained by excitatory input mechanisms operating between the left- and right-hemispheric PPAs.

In terms of relative activation strength, the data suggest that the effect of stronger activation for redundant as compared to mixed combinations might reflect a relative decrease for mixed conditions in the case of buildings and a relative increase for redundant stimulation in the case of faces. The coactivation model can account for this category-related difference, because interference or additive effects can be realised via facilitatory or inhibitory influences. Both

effects have been found in decision latencies in face recognition for stimulation in the opposite visual hemifield in an emotion detection task, where chimeric pictures of faces were shown to a blindsight patient: Responses were slowest for incongruent facial expressions presented to each visual hemifield compared and fastest for congruent information (deGelder et al., 2001).

The prolonged reaction time to incongruent category-information might be influenced by other processes than visual analysis, specifically when faces represented the incongruent category-information. Frontomedian areas were activated for mixed compared to redundant combinations for buildings but not for faces. This could indicate increased executive demands (Botvinick et al., 2004) for mixed conditions if buildings were the relevant category, maybe influenced by higher salience of faces acting as distractors (e.g. Lavie et al., 2003; Pollmann; 2000). The generally faster decision latencies for match trials of faces than for match trials of buildings further indicate, that detecting pictures of faces was 'easier' than detecting pictures of buildings.

5.5 Conclusion

In this experiment, effects of different input in the contralateral visual hemifield on activation differences in the PPA and FFA and their relation to possible behavioral effects in a category-detection task were investigated.

A RTE was observed, with category detection being performed faster for two pictures from the same category as compared to two pictures from different categories. The functional imaging data supports the assumption that this effect is at least partly based on enhanced activation in object-selective regions during bilateral input. The effect of an increased activation for bilateral redundant

compared to mixed stimulation generally indicated that input from both visual hemifields can contribute to activation of object-selective areas, independent of their lateralization. Enhanced executive demands for the mixed conditions might play an additional role for the behavioral effects. While the former seems to be independent of the category, the latter might be category-related.

The response properties in relation to unspecific category information in the opposite visual field differed between the FFA and PPA, and the underlying differences need further investigation.

In the following experiments, the effects of redundant stimulation will be investigated in comparison to word-picture combinations on PPA and VWFA activation. To ascertain that word- and picture-based responses can be disentangled in those areas, effects of preferred and unpreferred names on PPA and FFA activation will be analysed in a prior fMRI experiment.

6 Experiment 2

6.1 Introduction

The aim of this experiment was to investigate whether pictures and their written names elicit the same responses in object-selective areas. It was necessary to ensure that evoked neural responses to pictures and their names can be disentangled, because in the subsequent experiment, pictures and words will be used to investigate signal change in the object-selective areas of each hemisphere.

Evidence for activation of perceptual information during word reading comes from behavioral studies showing word-picture priming (Gordon & Irwin, 2000; Lebreton et al., 2001; Park & Gabrieli, 1995), and from imaging studies showing similar patterns of activation in left occipito-temporal cortex for objects and their denotations either during naming and silent reading (Bookheimer et al., 1995) or during semantic judgment tasks (Vandenberghe et al., 1996). It has further been shown that semantic processing of written words from different categories (animals and tools) can evoke category-related activation patterns in the fusiform gyri similar to those obtained during viewing and naming of pictures from the same categories (Chao et al., 1999; Perani et al., 1999).

Since the main interest was to know whether presentation of words leads to a rapid, automatic category-specific activation in the object-selective areas, presentation mode and task demands were chosen to favor shallow processing. To achieve this goal, pictures of faces and buildings and the corresponding words were presented

tachistoscopically in a rapid presentation event-related fMRI paradigm. Furthermore, the primary task of the subjects was a geometrical pattern detection task, for which the identification of the object pictures or words was not necessary. Under these conditions, activation in ventral occipital complex will be largely bottom-up driven, and top-down effects (Lamme & Roelfsema, 2000) will be small.

6.2 Materials and Methods

6.2.1 Participants

Ten volunteers participated in this study (5 males). All subjects were consistent right handers according to their score in the Edinburgh Handedness Inventory (Oldfield, 1971). The subjects' age was in the range of 20 to 37 years, with a mean age of 26.5 years. All subjects were native speakers of German and had no history of neurological or psychiatric disease. All subjects gave informed written consent according to the guidelines of the Max-Planck-Institute. The fMRI-procedures were approved by the University of Leipzig ethics committee.

6.2.2 Stimuli and Procedures

The experimental stimuli consisted of 30 color photographs and 30 black words on a white square that were presented on a gray screen (Fig. 6.1). For the building category, the pictures showed 15 different types of buildings; for the face category, the pictures showed 15 different human faces from various kinds of nationalities (see Appendix for a complete list of names). All faces were depicted in frontal view with about the same amount of hair and background visible. Pictures of faces were matched to the nationalities based on

facial attributes only, such as skin complexion, hair color, eye color, etc. The words were the corresponding descriptions for each picture, i.e. the names of the buildings and the names of the nationalities (e.g. 'church' and 'Chinese'). The names of the two categories did not differ with respect to frequency taken from the CELEX data base (Baayen et al. 1995), word length and number of syllables (all $p > 0.05$). Scrambled versions of all picture and word stimuli were generated using Fourier transformations on red, green, and blue components that left the spatial frequencies of the picture intact (<http://www.princeton.edu/~mpinsk/science.htm>).

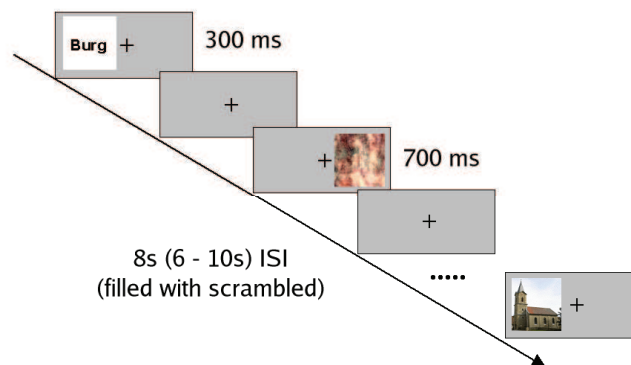


Figure 6.1 *Schematic illustration of the experimental paradigm. Critical trials of word and picture presentation in LVF and RVF were intermixed with 5-9 scrambled filler trials. On average, every 10th trial was a target detection trial, where Landolt-like rings had to be matched.*

In addition to passively watching the picture and word stimuli, subjects had to make a two-choice discrimination judgment based on two target stimuli. Pictures of two circles with a small gap on either the right or the left side were presented simultaneously and subjects had to decide as fast as possible whether the openings were in the same or opposite directions. This task was used to

ensure that subjects were fixating during the experiment, because identification of the gaps in both targets at once was only possible when fixating the cross in the middle.

All scans were performed in a single session with an absolute scanning time of about 20 minutes. Stimuli were presented through LCD goggles (VisuaStim XGA, Resonance Technology), with a virtual distance of 120 cm distance. A fixation cross was visible throughout the entire experimental block. For each trial a stimulus was presented for 300 ms followed by an intertrial interval of 700 ms during which only the fixation cross was visible. Pictures and words subtended about 5.7° of visual angle. The target circles had a size of about 1.9° visual angle and were presented in black on a white square of the same size. All stimuli were presented with their center located 4.5° to the right or left of fixation. Thus, the design of the experiment consisted of three factors (Format, Category and Visual hemifield) with two levels each (picture vs. word; building vs. face; right vs. left hemifield). Critical trials (presentation of a picture or a word) were embedded in sequences of scrambled stimuli. These 'filler' baseline trials were introduced to reduce the overlap of the BOLD-responses elicited by critical trials. In a previous study, it was demonstrated that blood-oxygenation-level-dependent (BOLD) signal changes related to the critical trials obtained in this way are as large as the difference between critical and baseline trials presented in isolation (Pollmann et al., 2000). The sequences of scrambled images ranged from 5 to 9 trials with the same mean and standard deviation of length for all conditions: on average each critical event was preceded and followed by seven trials of scrambled pictures. For the order of the critical events, the same critical condition was never repeated immediately. The transition probabilities were as balanced as possible in a way that the 15

repetitions per condition were followed by six of the remaining conditions twice and by one of the remaining condition three times. The identical stimulus was never instantly repeated (i.e. first in the right and then immediately in the left visual field or vice versa). There were no more than three consecutive repetitions of a single factor (e.g. no more than three pictures or words or three left-visual-field presentations). On average, every 10th trial (including scrambled 'filler' trials) was a target trial, with match and no-match trials randomly selected. Critical trials were never directly succeeded or followed by target trials, there was at least one scrambled 'filler' trial in between. While the intervals between target and critical trials varied from two to eight seconds, the average interval between critical and target stimuli was the same for all conditions. By rotating conditions, eight different sequences of the experimental phase were obtained that were balanced between subjects. During the course of the experiment, five null-events occurred where only the fixation cross was visible.

Subjects were instructed to passively watch the pictures and to read the words. The importance of keeping the cross fixated all the time was explicitly stressed. Eye movements were monitored online with a video camera by the experimenter. Trials in which a saccade occurred were marked by the experimenter and excluded from analysis. This was true for less than one percent of the critical trials.

At the beginning of the experiment, subjects were shown successively all pairs of matched pictures and words for 4 seconds each. After the experiment and outside the scanner, a recall test was given where subjects had to name all pictures. Subjects were then thanked for their participation and debriefed.

6.2.3 FMRI Procedure

After applying the procedures described at 4.3.2, baseline drifts were corrected by high-pass filtering, implemented using a discrete Fourier transform with a cut-off period of 50s. In the spatial domain, the data were filtered using a Gaussian filter with FWHM = 7 mm.

BOLD signal changes were analyzed for face and building selective activation in fusiform and parahippocampal gyri individually. For each participant, FFA and PPA in the right and left hemisphere were identified as regions selectively activated by pictures of buildings and faces close to the group coordinates in the same anatomical structure. In the LH, where two face-responsive peaks of activation were observed in the group data, the coordinates of the posterior center of activation corresponded better to commonly reported locations for the FFA in terms of Talairach coordinates as well as in terms of anatomical location, individual FFAs were determined starting from this point. Mean and standard deviation of coordinates are given in Table 6.1. FFAs and PPAs in both hemispheres could be localized in all subjects and reached statistical significance ($p < .05$) in nine out of the ten subjects for the right- and left hemispheric FFA and the left hemispheric PPA. For the right hemispheric PPA it reached statistical significance in half of the subjects (see Table 6.1). From the voxels of peak activation, time courses of the event-related BOLD signals were extracted from 0 – 10 seconds after stimulus onset and averaged across trials for each condition. The averaged signal time course obtained during the null-events was subtracted from the time course of each experimental condition. Percent signal change was then calculated relative to trial onset.

Depicted in the graphs (Figures 6.2 – 6.5) are grand-averages and standard error of the means for the trial-averaged time courses

based on an adjusted jackknife resampling technique (Ruge et al., 2003). Signal time courses were averaged across visual field for left and right FFA and PPA. Each of the ten subjects was then excluded from grand-averaging for each time point once. The resulting distribution of those ten grand-averages was then used to calculate the standard-error of the mean¹ that is indicated by the error bars.

Table 6.1: *Stereotactical coordinates (Talairach & Tournoux, 1988) of the individually obtained FFAs, PPAs, and VWFA.*

ROI	Hemisphere	N	Talairach Coordinates		
			x	y	z
PPA	left	9/10	-26 ± 5	-47 ± 7	-2 ± 4
PPA	right	5/10	24 ± 4	-44 ± 8	-5 ± 3
FFA	left	9/10	-39 ± 3	-59 ± 9	-8 ± 5
FFA	right	9/10	38 ± 3	-48 ± 6	-12 ± 4
VWFA (a)	left	7/10	-42 ± 4	-58 ± 6	-4 ± 3
VWFA (b)	left	10/10	-38 ± 5	-67 ± 5	-5 ± 3

Coordinates are mean ± SD in the space of the Talairach and Tournoux brain atlas and based on all subjects. N= number of subjects who showed significant activation of ROI ($p < 0.05$). Individual VWFAs were identified for the contrast of words against a) scrambles pictures and b) fixation baseline.

6.3 Results

6.3.1 Behavioral Results

On the target discrimination task, subjects performed well above chance ($T_9 = 3.893$, $p < .01$) with a mean of 64% correct answers.

In the post-experimental questionnaire, subjects were asked to name the 30 pictures of faces and buildings that had previously appeared in the experiment with the appropriate term. On average, subjects were able to give a correct answer for about 70% (69,7%;

¹ Jackknife algorithm for the standard-error of a mean: $se = \sqrt{\frac{N-1}{N} \sum_{i=1}^N (x(i)_{-1} - X)^2}$ with $x(i)_{-1}$ representing the grand-averages without subject i and X representing the mean of all grand-averages.

SD=7.3%), i.e. they could correctly name 21 out of the 30 pictures. The most difficult to name was the face depicting the 'Franzose' ('Frenchman'), only two subjects could give a correct answer. 'Mühle' ('mill') and 'Schwedin' ('Swede', f.) were correctly identified by all subjects, 'Mongole' ('Mongolian'), 'Schotte' ('Scotsman'), 'Ire' ('Irishman') and 'Stadion' ('stadium') also posed little problems, with nine correct identifications each.

6.3.2 Imaging Results

Identification of FFA and PPA

Consistent with previous reports, regions in ventral occipito-temporal cortex could be identified that were selectively activated by pictures of the two stimulus categories. Directly comparing pictures of faces with pictures of buildings, bilateral regions in the fusiform gyrus responded more strongly to pictures of faces than pictures of buildings, whereas a region in the left parahippocampal gyrus showed the opposite pattern ($p < .001$ in all cases). The right FFA was located at 37x -50y -12z; in the left hemisphere, two foci of activation were observed, one more anterior (-38x, -38y, -12z) and one more posterior (-41x, -50y, -14z). The left PPA was found at -32x, -47y, -2z. Because of the strong hypothesis about the location of an homologous area activated specifically by pictures of buildings in the right parahippocampal gyrus, the threshold was lowered to $p = 0.005$, and the corresponding PPA in the right hemisphere could be identified at 8x, -48y, 0z (Fig. 6.2).

The Talairach coordinates (Talairach & Tournoux, 1988) for the centers of activation were consistent with the ones reported in numerous previous studies for both the FFA (Chao, et al., 1999; Gauthier et al., 2000; Ishai et al., 1999, 2000; Kanwisher et al.,

1997) and the PPA (Epstein & Kanwisher, 1998; Epstein et al., 1999; Gorno-Tempini & Price, 2001; Ishai et al., 1999). For instance, contrasting pictures of houses with pictures of faces, Haxby and his colleagues (Haxby et al., 2001) found activation peaks for face-selective regions at -27x, -51y, and -14z in the left and 4x, -55y, and -12z in the right hemisphere; for house-selective areas coordinates of -39x, -55y, and -16z in the left and 39x, -59y, -16z in the right hemisphere were reported.

Signal time course analyses

Time course analyses FFA

Repeated measures analyses of variance (ANOVA) were conducted with Time (timepoints 0 to 10), Category (face, building) and Format (picture, word) as factors. For the right FFA significant main effects of Time [$F_{(10,90)}=8.23$; $p<0.05$], Category [$F_{(1,9)}=20.19$; $p<0.05$] and Format [$F_{(1,9)}=8.21$; $p<0.05$] were obtained along with a significant interaction between Category and Format [$F_{(1,9)}=13.32$; $p<0.05$]. Analyzing category-differences separately for both types of stimulus format yielded a main effect of Category for pictures [$F_{(1,9)}=19.43$; $p<0.05$], but not for words [$F_{(1,9)}=0.11$; $p>0.05$]. For face stimuli the peak response in the right FFA was higher if the face was presented as picture (amplitude of 0.81% signal change) than if it was presented as word naming the face (0.29%). For building stimuli the response was as strong for pictures (0.29%) as for names (0.3%; see Fig. 6.2). Activation elicited by pictures of buildings was similar to activation elicited by words from both categories (all about 0.3%).

For the left FFA the ANOVA showed comparable effects. The main effects of Time [$F_{(10,90)}=6.43$; $p<0.05$] and Category [$F_{(1,9)}=14.5$; $p<0.05$] were significant. The main effect of Format was not significant [$F_{(1,9)}=1.74$; $p>0.05$], but, more importantly, the interaction

between Category and Format was highly significant [$F_{(1,9)}=29.52$; $p<0.05$]. In two different analyses for words and pictures, again, a main effect of Category was obtained for picture stimuli [$F_{(1,9)}=47.89$; $p<0.05$] but not for word stimuli [$F_{(1,9)}=0.02$; $p>0.05$]. As for the right FFA, in the left FFA the response to pictures of faces was higher in amplitude (0.56%) than the response to names of faces (0.33%), whereas no difference was obtained for the pictures and names of buildings (0.29% and 0.32%; see Fig. 6.2). Again, words and non-preferred pictures elicited similar signals (all about 0.3%).

Taken together, these results show that both FFAs responded differentially to the pictures of the two categories, but equally to the words of both categories. Since the ROIs were identified in reference to their selectiveness for pictures of the two categories, it is not surprising that in both FFAs pictures of faces elicited higher activation than pictures of buildings. However, the ROIs were identified solely based on the contrast that included conditions of picture presentation. Therefore, the selection process was completely independent of activation that followed word presentation and cannot account for any differences between the word conditions. Comparing percent signal change between right and left FFA, the difference in amplitude for pictures of faces is considerably higher in the right (0.81%) than in the left (0.56%) hemisphere. For words of faces and words of buildings, the amplitudes are similar in both hemispheres (all about 0.3%).

Time course analyses PPA

The analogous ANOVAs were carried out for the right and left PPA as regions of interest. They yielded a comparable pattern as for the face-responsive areas, only that in these analyses pictures of buildings elicited stronger activation than pictures of faces. For the

left PPA the ANOVA showed a significant main effect of Category [$F_{(1,9)}=11.86$; $p<0.05$], a marginal main effect of Format [$F_{(1,9)}=5.06$; $p=0.051$] and an interaction between Category and Format [$F_{(1,9)}=5.26$; $p<0.05$]. In two different analyses for words and pictures, a main effect of Category was obtained for picture stimuli [$F_{(1,9)}=11.38$; $p<0.05$] but no effect of Category was obtained for word stimuli [$F_{(1,9)}=0.65$; $p>0.05$]. The peak activation for pictures of buildings was higher (0.4%) than for pictures of faces (0.15%), whereas there was no differences in amplitude height for names of faces (0.1%) and names of buildings (0.07%). Words of both categories and pictures of the non-preferred category, again, evoked comparable, very small signal increases (about 0.1%). As can be seen in Figure 6.2, the variance for pictures of buildings was relatively high. Excluding one of the subjects who showed an unusually high signal change for pictures of buildings lowered the average signal change for pictures of buildings to about 0.23%, however the difference in signal change between the conditions stayed the same and the statistical analyses showed significant effects for Category [$F_{(1,9)}=10.43$; $p<0.05$], Format [$F_{(1,9)}=9.11$; $p<0.05$], and a significant interaction between Category and Format [$F_{(1,9)}=16.18$; $p<0.05$]. Again, tested separately, there was a main effect of Category for pictures [$F_{(1,9)}=15.46$; $p<0.05$], but not for words [$F_{(1,9)}=0.18$; $p>0.05$]. There were no other outliers in the remaining ROIs.

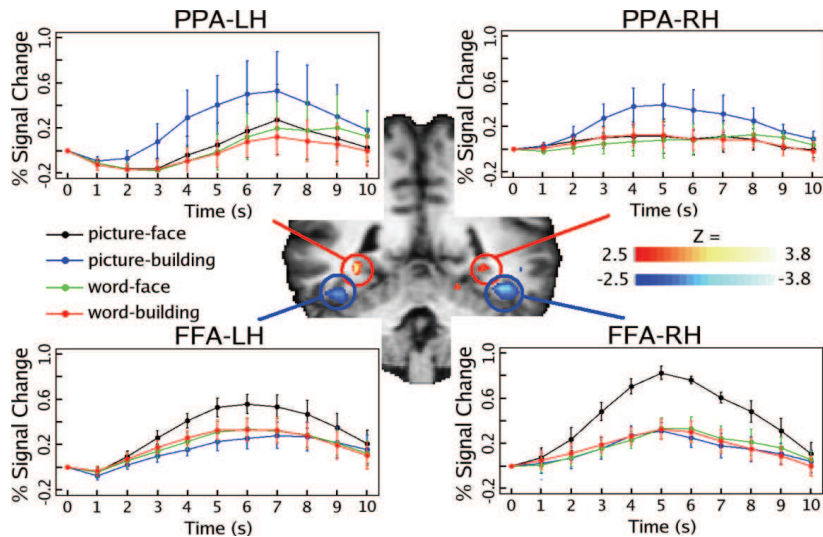


Figure 6.2 Changes of the hemodynamic response to word- and picture-conditions for the four regions of interest (left and right hemispheric FFA and PPA). The activations represent the group average for contrasting building pictures with face pictures. Left hemisphere is on the left. The picture plane is at $y = -47$. The red-yellow color scale indicates stronger responses elicited by houses than faces, the blueish scale indicates the reverse, stronger responses to faces. Time courses are based on individual ROIs. Depicted are mean signal changes and standard-errors of the mean (see Methods).

For the right PPA there was a significant main effect of Category [$F_{(1,9)}=10.48$; $p<0.05$], but the interaction between Category and Format was only marginally significant [$F_{(1,9)}=4.41$; $p=0.065$], as was the main effect of Format [$F_{(1,9)}=4.42$; $p=0.065$]. Nevertheless, analyzing category-differences separately for both types of stimulus format, a main effect of Category was obtained for pictures [$F_{(1,9)}=18.45$; $p<0.05$] but not for words [$F_{(1,9)}<0.01$; $p>0.05$]. Again, there was a higher response to pictures of buildings (0.32%) than to pictures of faces (0.06%), with no differential responses to the categories of names (for buildings 0.08%, for faces 0.06%). Thus, signal change for pictures of faces and words of faces and buildings were all negligible.

In contrast to amplitude differences between the hemispheres in the FFA, the percent signal change for pictures of buildings was similar in left and right PPA, with a slight tendency for higher activation in the left hemisphere (0.4% and 0.32%). The amplitude for the names of buildings was very similar in both right and left hemisphere (0.07% and 0.08%).

In summary, time course analyses revealed that areas selectively activated for pictures of each category did not respond differentially to words denoting preferred versus non-preferred pictures. Instead, they responded similarly to all word stimuli and pictures of non-preferred categories.

To examine possible sex differences, the same analyses were run with Sex as a between-subjects factor, however, no significant main effects of Sex or interactions with this factor were found.

Although not the main focus of the experiment, when effects of Visual Hemifield were investigated, there were no significant main effects or interactions with Visual Hemifield for the left and right hemispheric PPA and the right hemispheric FFA in the overall analyses. For the left hemispheric FFA, there was a main effect of Visual Hemifield [$F_{(1,9)}=9.91$; $p<0.05$] along with a Format by Visual Hemifield interaction [$F_{(1,9)}=6.23$; $p<0.05$], but the Category by Format interaction did not interact with Visual Hemifield [$F_{(1,9)}=0.15$; $p>0.05$]. The interaction of Format with Visual Hemifield was based on no effect of Visual Hemifield for words [$F_{(1,9)}=0.05$; $p>0.05$], but a main effect of Visual Hemifield for pictures [$F_{(1,9)}=15.08$; $p>0.05$] that did not interact with Category [$F_{(1,9)}=0.75$; $p>0.05$]. While pictures presented contralaterally led to higher amplitudes (0.46%) than pictures presented ipsilaterally (0.39%) in the left hemispheric FFA, this was the same for pictures of buildings and faces.

Word-Related activity

Contrasted against scrambled pictures ($p < 0.001$), words most strongly activated an area in the left inferior occipital gyrus, bordering the lateral occipitotemporal sulcus (Talairach coordinates: $-41x$, $-62y$, $-3z$; see Figure 6.3). This location corresponds closely to previous reports of word-specific activation corresponding to the 'visual word form area' (VWFA, Cohen et al., 2000). Based on recent findings, McCandliss et al. (2003) reported that activation for words can be reliably found within the left occipitotemporal sulcus bordering the fusiform gyrus.

Although left lateralized, Cohen et al. (2000) demonstrated that the VWFA is activated by contralateral as well as ipsilateral presentation of words, a finding that could be replicated in this study: words presented in the LVF and words presented in the RVF yielded very similar activation peaks (left VF: $-44x$, $-62y$, $-3z$, $p < .005$; right VF: $-41x$, $-60y$, $-3z$, $p < .001$; see Figure 6.3). In absolute values, a somewhat stronger activation for words presented contralaterally was observed in the left-hemispheric VWFA.

As for the object-selective areas, ROIs based on individual contrasts were obtained for each subject, in 7 out of 10 subjects this activation was significant with $p < .05$ (see 6. 1). The individual VWFAs were all located along the left lateral occipito-temporal sulcus, with a focus in the lateral occipito-temporal sulcus (5 out of 10), the lateral occipito-temporal gyrus (4 out of 10), and the fusiform gyrus (1 out of 10). Thus, activations found in this study were grouped along the lateral bank of the lateral occipito-temporal sulcus, in contrast to the locations along the medial bank as reported in a meta-analysis of McCandliss et al. (2003). However, this meta-analysis is based on eleven studies that used different contrasts, which can influence the exact location of the VWFA (Cohen et al.,

2000). In most studies (8 out of 11) written word conditions were contrasted with relatively sparse visual input, i.e. fixation, resting, '****' or '+++' presentation, and activation peaks in left fusiform gyrus were obtained in all but one study (Beauregard et al., 1997; Brunswick et al. 1999; Buckner et al., 2000; Fiez et al., 1999; Kiehl et al., 1999; Paulesu et al., 2001; Price et al., 1996; Wagner et al., 1998). In the remaining three studies, more complex visual input was used as baseline (textures, geometrical figures and letters), and word specific activation was found not in the fusiform gyrus but at the lateral temporal-occipital junction in two out of three studies (Puce et al., 1996; Xu et al., 2001; but not Tagamets et al., 2000). Contrasting trials of word presentations with trials of null-events (i.e. fixation), the peak activation for words (see Figure 6.3 and Table 6.1, VWFA(b)) shifted medially and was found in the middle fusiform gyrus (-32x, -62y, -8z), indicating that the word-specific processing in this experiment was comparable to previously reported data.

For the individually defined voxels with peak activation of the word against scrambled pictures contrast, ANOVAs were calculated with Format (picture, word), Category (building, faces), Visual Hemifield (right, left), and Time (time points 0 -10, i.e. 11 seconds) as factors. These ANOVAs revealed a main effect of Format [$F_{(1,9)}=5.48$; $p<0.05$] and Time [$F_{(1,9)}=13.98$; $p<0.05$], but no effect of Category [$F_{(1,9)}=1.8$; $p>0.05$], no effect of Visual Hemifield [$F_{(1,9)}=0.28$; $p>0.05$], and no interaction between Format and Category [$F_{(1,9)}=0.04$; $p>0.05$]. The peak activation for words was higher (0.52%) than the peak activation for pictures (0.42%; see Figure 6.3).

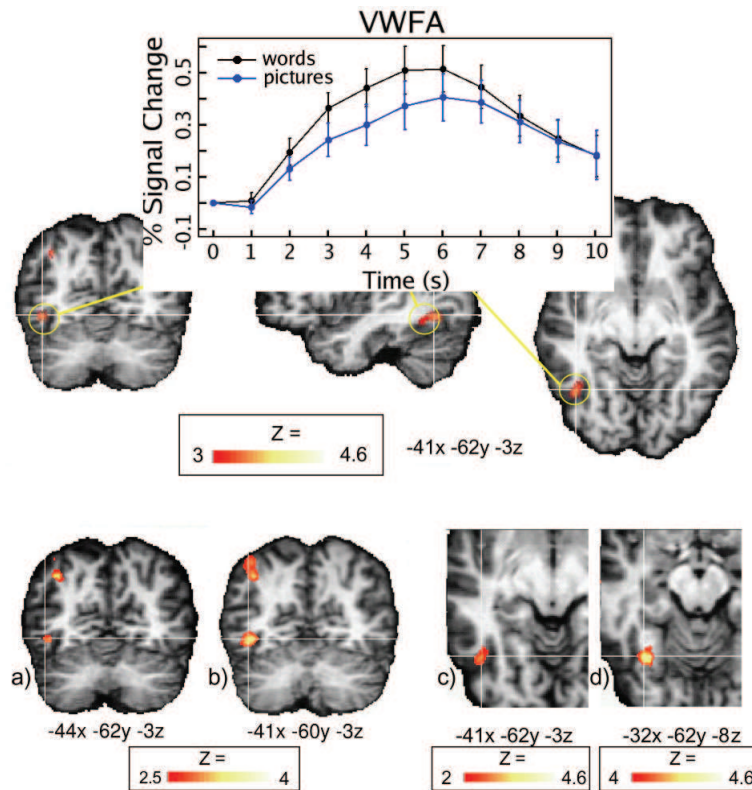


Figure 6.3 Changes of the hemodynamic response to word- and picture-conditions for the area that responded maximally to words. The group activation represents the contrast for words against scrambled pictures. Time course data is based on individual ROIs. Depicted are mean signal changes and standard-errors of the mean (see Methods). Bottom: The activation for this area was almost identical in location for presentation in the LVF (a) and the RVF (b). Contrasted against the scrambled picture baseline word activation was found at the lateral bank of the lateral occipito-temporal sulcus, in the lateral occipito-temporal gyrus (c), whereas contrasted against fixation baseline word activation was found along the medial bank of the lateral occipito-temporal sulcus, in the fusiform gyrus (d). Left hemisphere is on the left. Colorscales indicate z-scores.

Testing words and pictures separately with Category, Visual Field and Time as factors, no effects of Category or Visual Field nor an interaction between Category and Visual Field were obtained in either analysis. Thus, this region was activated more strongly by words than pictures independent of hemifield of presentation and category. When Sex was included as between-subject factor in the

same ANOVAs for separately testing the activation elicited by pictures and words in the VWFA, no significant main or interaction effects with the factor Sex for pictures were observed. For words, there was no significant main effect of Sex [$F_{(1,8)}=0.59$; $p>0.05$] and no main effect of Visual Field [$F_{(1,8)}=0.24$; $p>0.05$], but a significant interaction between Sex and Visual field [$F_{(1,8)}=25.68$; $p<0.05$]. While female subjects showed higher activation for words presented in the right than in the left visual field, there was no such difference for the male subjects (Fig. 6.4).

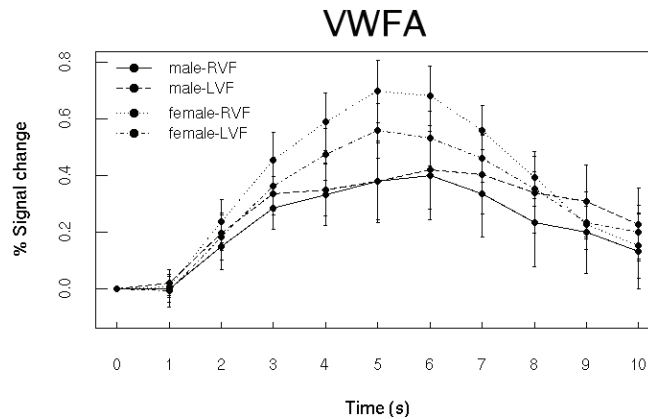


Figure 6.4 Sex differences in VWFA. Time courses are based on individual ROIs. Depicted are mean signal changes and standard-errors of the mean (see Methods).

In spite of their adjacent location in the occipito-temporal cortex of the left hemisphere, peaks of activation for FFA and VWFA (contrasted against scrambled pictures or fixation baseline) were not identical in location, neither if activation was averaged over subjects (see Figure 6.5), nor in the individually analyzed data. In the individual data sets, peaks of activation for the VWFA were always located more dorsally than the left FFA. Comparing the BOLD signal changes for word and picture conditions in these two areas, in the left FFA signal changes during conditions of word presentation were

not different from signal changes during conditions of non-preferred picture presentations. There was a trend for pictures of faces to elicit a stronger response in the VWFA than pictures of buildings (again, no significant effect of Category was obtained analyzing the time courses of picture-related signal change in the VWFA; $F_{(1,9)}=0.7$; $p=0.424$).

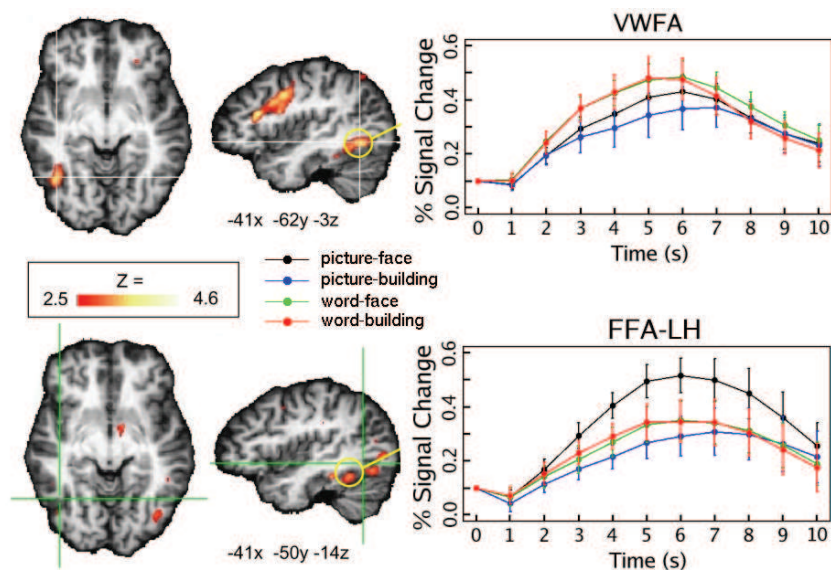


Figure 6.5 Comparison of face- and word-specific activation. Cross-hairs indicate the location of the VWFA. Upper row: contrast of words against scrambled pictures baseline; lower row: contrast of pictures of faces with pictures of buildings. Red indicates stronger responses elicited by pictures of faces than pictures of buildings. Time courses are based on individual ROIs. Left hemisphere is depicted on the left. Colorscales indicate z-scores.

6.4 Discussion

The activation elicited by pictures of faces and buildings replicated the pattern described in numerous imaging studies. Pictures of faces activated most strongly regions in the lateral fusiform gyrus. Face selective activations could be identified in both hemispheres, but

with stronger activation in the RH. The same laterality difference in activation strength has been reported before (e.g. Kanwisher et al., 1997; Puce et al., 1996). Pictures of buildings activated most strongly regions in the parahippocampal gyrus, bilaterally, although the activation was stronger in the left hemisphere.

Words, however, did not yield a comparable pattern of activation. In regions that showed category-specific activation for pictures of faces and buildings, consistent with previously reported locations of the FFA and PPA, no comparable category-specific activation for words was observed. In contrast, words corresponding to both categories elicited only minor activation of comparable strength as pictures of the non-preferred category. This pattern of activation did not differ between the hemispheres.

In contrast to this data, evidence for shared activation of pictures and their written names comes from imaging studies demonstrating that pictures and words of the same objects activated largely overlapping areas (Bookheimer et al., 1995; Chee et al., 2000; Vandenberghe et al., 1996). In one PET study, unrelated vocal responses were given during viewing of pictures and their written labels and then contrasted with conditions where the pictures had to be named and the words read. Two regions within the left ventral occipital cortex were found to be activated differentially by task and by stimulus format, and one region in the left anterior fusiform gyrus was equally activated by words and objects (Moore & Price, 1999). Similarly, Chinese characters, English words, and pictures containing the same meaning commonly activated left temporal areas and the left fusiform gyrus during a semantic matching task. Additionally, while semantic processing of Chinese characters and English words shared similar activations, there was stronger right occipital activation during semantic processing of pictures compared

to either word or character processing (Chee et al., 2000). Yet in these studies, no differentiation was made between different categories of pictures or words. Chao and her colleagues found a comparable lateral-to-ventral topography of activation in bilateral fusiform gyri contrasting animals and tools during picture naming as well as during semantic processing of their written names (Chao et al., 1999). Similarly, comparing animals to non-living entities elicited activation in left occipital and temporal cortex during word as well as during picture processing (Perani et al., 1999). In contrast, in a 'same' versus 'different' matching task Gorno-Tempini et al. (1998) found different activations in occipital and temporal areas when pictures of faces and their written proper names were presented. Processing of pictures resulted in stronger activation in fusiform gyri and right lingual gyrus and processing of names lead to enhanced activity in left temporal cortex. Commonly activated were regions in temporo-polar and frontal cortex. While it has been reported that lesions in FFA and PPA are associated with impairments in recognizing pictures of faces (Wada & Yamamoto, 2001) and buildings (Aguirre & D'Esposito, 1999), data on concomitant loss of category-specific semantic knowledge is rare, but seems to be associated with more anterior lesions in the temporal lobe (see Gorno-Tempini et al., 1998).

One mediating process why reading the written name of an object could lead to activation of picture processing areas is mental imagery. It is still under debate whether mental imagery and visual perception share exactly the same forms of representation (Pylyshyn, 2003) and if early visual areas are always involved in imagery, there is evidence that the visual cortex can be activated through mental imagery alone (see Kosslyn et al., 2001 for a review). Under explicit mental imagery instructions, FFA and PPA

showed significant activation during visualization of faces and scenes, respectively, indicating that retinal input is not a prerequisite for specific responses in this cortical region (Ishai et al., 2002; O'Craven & Kanwisher, 2000). Activation of the FFA under imagery instructions has been found in conditions where specific images of faces had to be recalled from pictures recently seen. Moreover, activation has been reported in conditions where subjects had to generate a corresponding face when only the name of a celebrity was given (Ishai et al., 2002). Although identical in location, activation of FFA and PPA has often been reported to be smaller during imagery than during perception (Ishai et al., 2002; O'Craven & Kanwisher, 2000).

In the above mentioned studies (Bookheimer et al., 1995; Chao et al., 1999; Chee et al., 2000; Perani et al., 1999; and Vandenberghe et al., 1996) showing similar activation for pictures and words, tasks involved matching, reading, and answering questions about the presented objects, i.e. more elaborate processing than the passive viewing of briefly presented stimuli required in this experiment. In contrast to these studies, this experiment favored shallow word processing. Words were presented tachistoscopically at peripheral locations. Moreover, although participants were instructed to pay attention to the pictures and to read the words, their primary task was to detect and compare geometrical target items which were randomly presented. All of this may have prevented them to process the words to a 'deep', semantic level (Craik & Lockhart, 1972). This was not unintentional. Rather than replicating previous reports of mental imagery-related activation in occipital cortex, the main interest of this experiment was the question, whether presentation of words automatically leads to activation of the corresponding visual object processing areas. Data from this experiment shows that this

is not the case. When briefly reading the names of faces or buildings, activation in occipito-temporal regions selectively responding to the pictures of faces or buildings does not occur automatically. Recently, the crucial role of semantic elaboration for category-specific activation in posterior regions of the fusiform gyrus could be demonstrated for written names of animals and tools (Devlin et al., 2005).

In the discussion about mental imagery, Farah (1995) has suggested that controlled top-down processes and attention are involved when images are created from long-term memory during mental imagery. Evidence for top-down processes in the reactivation of visual information from word stimuli comes from an ERP study (van Schie et al., 2003). Only later (P2 and P3 components) but not early ERP components (P1 and N1) were influenced when words had the same instead of a different meaning than pictures preceding at the same location. Similarly, in a property verification task using written stimuli with no explicit mental imagery instruction, Kan et al. (2003) found activity in left fusiform gyrus only in conditions where conceptual processing was supposed to be necessary, because words on true and false trials were equally associated. No activation in this area was found when lexical association between the words was sufficient to answer correctly. Further indication for a prerequisite role of top-down mediation for activation in object-selective areas comes from dynamic causal modeling of visual perception and visual imagery of faces, houses, and chairs (Mechelli et al., 2004). Category-selective activation in occipito-temporal cortex was associated with increased connectivity from early visual areas during visual perception, but with increased connectivity from prefrontal cortex during visual imagery.

Consistent with these imaging findings, in behavioral studies the amount of conceptual processing of the written words influences the magnitude of subsequent word-picture priming. For instance, Hirshman et al. (1990) found that generating but not reading the name of an object lead to faster identification of the corresponding picture (but see Srinivas, 1992). Similarly, McDermott and Roediger (1994) demonstrated that the instruction to imagine corresponding pictures during word reading enhanced fragment identification of these pictures later on, but simply rating the pleasantness of the words did not.

The general absence of sizable word-related activation in the FFA and PPA in this study could be due to the fact that participants were not able to process the words at all. The relatively low performance in the behavioral task could suggest that subjects had difficulties in recognizing the stimuli. A general inability to perceive the words, however, can be ruled out, because word-specific activation was found along the left lateral occipito-temporal gyrus. This, however, does not mean that the VWFA activation proves conscious understanding of word reading. Comparable activation has been observed for masked words, which could not be discriminated as words or names (Dehaene et al., 2001). Nevertheless, the word-specific activation along the left lateral occipito-temporal sulcus shows that words were differentially processed from pictures. The peak of activation in the contrast against scrambled images was observed more laterally than VWFA activation sometimes reported in the literature (Cohen et al., 2000). However, the contrast against the fixation baseline showed a peak of word-related activation more medially in the medial bank of the lateral occipito-temporal sulcus. Thus, the general location for the VWFA in this study is consistent

with previous reports on word specific activation (McCandliss et al., 2003).

In accordance with previous findings (Cohen et al., 2000), VWFA activation was hemifield-independent (Fig. 6.3 a) and b). Analyzing the time courses of percent signal change, there was no main effect of Visual Field, but a significant interaction between Sex and Visual Field for words in the VWFA. While words presented in the RVF lead to higher activation than words presented in the LVF for the female subjects, this preference for contralaterally presented words was absent in the male subjects. Greater hemifield independence for written words in male subjects is in line with previous reports on sex differences in language representation where men show stronger left-lateralized activation (e.g. Rossell et al., 2002). However, a recent meta-analysis did not confirm these sex differences in language lateralization (Sommer et al., 2004). Hence, additional studies and greater sample sizes are necessary to further investigate possible sex differences in VWFA activation.

No reliable effects of Visual Hemifield in the time course analyses of the FFA and PPA was found, apart from higher activations in the left hemispheric FFA for pictures presented contralaterally. However, it might be possible that since it was not the main focus, the power of this design was too limited to detect potential hemifield differences in processing contra- and ipsilaterally presented pictures in object-selective areas.

The word-specific activation in the absence of category-specific effects of word reading in the FFA and PPA supports the concept of a prelexical processing related to the VWFA (Cohen et al., 2000, 2004; McCandliss et al., 2003; but see Price & Devlin, 2003). The VWFA is thought to be sensitive 'to specific and abstract qualities of visual word forms that are not easily attributable to more basic

stimulus properties, and are also separable from higher-order linguistic properties' (McCandliss et al., 2003, p. 293). This description fits very well to the observation of a left occipito-temporal word-specific activation in the absence of category-specific effects in the FFA and PPA, which may be expected to be present when the words would have been processed to a deeper semantic level, including visual imagery (Devlin et al., 2005). McCandliss et al. (2003) propose that the VWFA supports a 'level of perceptual processing that extracts invariant information about the structure of visual words and integrates this information into a perceptual object' (p. 293). Interestingly, if 'visual words' is replaced by 'visual images of faces (or buildings)', the same explanation could be applied to the activations of the FFA and PPA. In this way, the activations found for pictures of faces and buildings and for written words may reflect a comparable processing stage in the respective areas of the occipital lobe.

6.5 Conclusion

In summary, the present fMRI study has confirmed that faces and buildings differentially activate regions within the ventral visual stream. The written labels of pictures from the preferred category, however, did not lead to responses any different from pictures or words of the non-preferred category in these areas. These results indicate that there are conditions under which, e.g. reading the word 'castle' is not the same as seeing the picture of a castle, at least with respect to the FFA and PPA. They also suggest that mental imagery is not induced automatically during single word reading in a passive viewing task, but rather depends on semantic processing or cognitive control mechanisms. This is especially relevant for further studies investigating differences and similarities in processing

pictures and their written names, because the amount of deep semantic processing can be controlled experimentally, e.g. by varying task demands. This will be done in the next experiment, where pictures and names of buildings will be presented once under a comparable passive viewing condition and once under a semantic matching condition.

7 Pretests

7.1 Evaluation of Stimulus Material

The pictures of buildings and their respective names were evaluated in two questionnaires by two independent groups. One of the questionnaires was used to confirm that the pictures of buildings could be identified easily with respect to the specific type of building. The other questionnaire was used to rule out that the names of different types of buildings varied largely in their imageability, since imagination of written names could a) account for different effects of written word processing in the PPAs and b) induce different strategies during matching to the associated pictures.

To ensure that pictures were identifiable at the relevant categorizational level, pictures were validated in a naming questionnaire. 55 subjects aged between 19 and 36 years (mean age=22; SD=3.34) were given a list containing the 40 pictures of buildings used in the experiment. Subjects were requested to name the buildings depicted, without explicitly stressing the categorizational level, but examples were given when necessary. The appropriate level of naming was used in all subjects. 76% of all answers matched to the name labels that were used for the experiment. The picture with the greatest deviation from the assigned label was one of the pictures from the category 'Laube' ('arbour'). Only 7% of all subjects named the object as expected, 66% called it 'Pavillon' instead. 'Pavillon' itself was not used in the experiment and can be seen as synonym for 'Laube', i.e. the poor proportion of correct answers should not have a substantial negative

impact on the ability to make a correct semantic matching decision. Buildings like 'bridge', 'tent' or 'garage' were named as expected by more than 95% of the subjects.

To rule out that large differences in imageability for the names of the different types of buildings existed, the imageability of the different category names used in the experiment was assessed with a questionnaire. 36 subjects (29 female, 7 male) aged between 18 and 41 years, with a mean age of 24, rated all words used in the experiment on a 5-point-scale of imageability ranging from 1 ('hardly imageable') to 5 ('highly imageable'). Generally, all words could be imaged well with the average imageability rating being 4.22. According to the subjects' assessment, 'tent' could be imagined best (average 4.83), followed by 'bridge' (4.81) and 'church' (4.78). The most difficult name of building to visualize was 'temple', reaching an average of 3.31 ('moderately imageable') on the scale.

7.2 Behavioral Pretests of Two Variations of the Semantic Matching Task

Two behavioral studies were conducted before the fMRI data collection to evaluate two different versions of semantic matching paradigms. Both experiments used for the behavioral pre-testing were semantic matching tasks on pictures and words, but they differed in the categorizational level of matching. In Experiment A, subjects were instructed to make a matching decision only within the category of buildings, i.e. a specific type of building had to be identified as word or picture (e.g. church, tower, bridge, etc.). In Experiment B, pictures and names of buildings and faces were shown, and subjects had to make a matching decision based on the general category (i.e. face or building). For the within category matching task, pictures of buildings were used, because naming

types of buildings might be easier and less ambiguously than naming the nationality of faces.

7.2.1 Stimuli and Procedures

Stimuli were presented bilaterally, one stimulus in each visual hemifield. Words and pictures were combined with each other, resulting in four different stimulation conditions (word-picture (WP), picture-word (PW), word-word (WW), picture-picture (PP), according to the LVF-RVF ordering). In Experiment A, words and pictures were all different types of buildings, in Experiment B, words and pictures were buildings and faces (i.e. nationalities). For the picture-picture conditions, always two different pictures were presented, i.e. two different pictures showing the same exemplar for the buildings (e.g. two different churches), and two different exemplars for the matching of faces and buildings (e.g. a church and a bridge). Similarly, for the word-word conditions, the identical word was presented in the building category (e.g. church), but once in upper- and once in lowercase letters. In the face and building matching task, two different names from the same category were presented. The stimuli used in the pre-testing were the pictures used in the first and second fMRI experiment in a gray scale version. Five additional exemplars were added to the category of buildings used in the first fMRI-Experiment (Chapter 5). Words were presented in black on scrambled backgrounds with different fonts and a matched length of signs, i.e. words were surrounded by number signs (“#”) to obscure possible length effects. Stimuli were presented for 300ms in the LVF and RVF simultaneously. The inter-stimulus-interval between critical trials was filled with series of scrambled picture presentations of different length (see stimulus und procedure section in the next chapter for additional details). Subjects responded with the index

finger to indicate match trials and with the middle finger to indicate mismatch trials. The response hand was changed after the first block of the experiment, with the order counterbalanced across subjects. Nine subjects were tested in single sessions in Experiment A and Experiment B, respectively.

7.2.2 Results

Experiment A

The results of a multivariate ANOVA with Condition (PW, WP, WW, PP) and Match (match, mismatch) as independent variables yielded an only marginally significant main effect on reaction times for correct answers for Condition [$F_{(3,6)}=4.42$, $p=0.58$] and a significant main effect for Match [$F_{(1,8)}=52.24$, $p<0.05$]. The interaction between both factors did not reach significance [$F_{(3,6)}=1.62$, $p>0.05$].

Even though the main effect of condition proved only marginally significant, multiple comparisons were performed on the mean reaction times averaged across match and mismatch trials. The results of the post-hoc t-test revealed significantly faster reaction times to picture-word conditions than to word-word and picture-word conditions ($p<0.05$, Bonferroni-Holm corrected, see Figure 7.1).

Experiment B

A multivariate ANOVA was carried out on reaction times for correct responses, with Condition (PW, WP, WW, PP), Match (match, mismatch), and Category (face, building) as independent variables. The analysis yielded a significant main effect for condition [$F_{(3,6)}=4.89$, $p<0.05$], for match [$F_{(1,8)}=10.56$, $p<0.05$], and for category [$F_{(1,8)}=10.37$, $p<0.05$], but no significant interactions. Corrected comparisons on reaction time averaged across match and mismatch trials and averaged across faces and buildings showed

that reactions to picture-picture stimuli were significantly slower than reactions to all other stimulus types, no other differences reached significance.

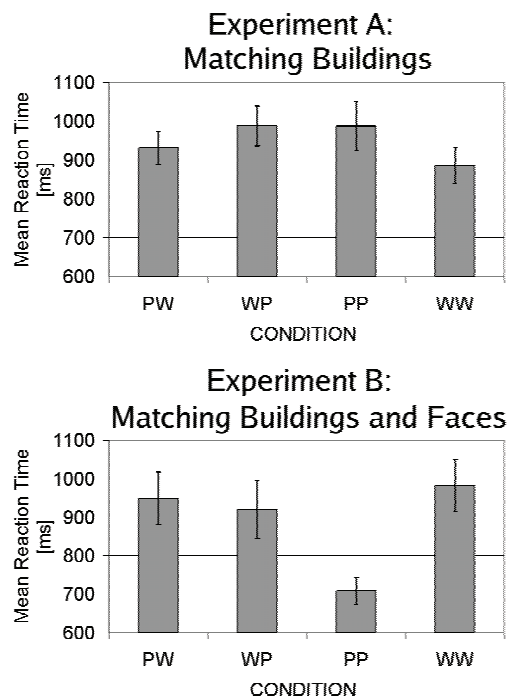


Figure 7.1 Behavioral results of two experiments, where pictures and words had to be semantically matched within the category of buildings (top; Experiment A) and at the between categorical level of faces and buildings (bottom; Experiment B).

The main purpose of the behavioral experiments was to select one of these two experimental paradigms for the fMRI scanning session. In Experiment A, the expected effect of more efficient matching for words presented in the RVF compared to LVF presentation was obtained, which was absent in the Experiment B for no apparent reason. Furthermore, in Experiment B, picture-picture conditions were matched much faster than word-word or

picture-word combinations. This large difference in reaction time could hint to qualitatively different decision processes in matching two pictures from the same category compared to matching pictures and words, e.g. detecting faces might be possible at lower levels of visual analysis than identifying a word as a name of a building or of a nationality. Therefore, Experiment A appeared to be more sensitive to hemispheric specialization for the matching of pictures and words, and was consequently selected to be conducted in the scanning session. The stimuli of Experiment A were further improved (see next Chapter for details) to avoid matching strategies based on low-level physical characteristics instead of semantic content, because words that match have the same meaning (e.g. church) under this experimental condition.

8 Experiment 3 – Effects of Bilateral Stimulation and Semantic Matching

8.1 Introduction

In this event-related fMRI experiment, pictures and written names of buildings were presented tachistoscopically in lateralized displays. Responses of the PPAs and VWFA to ipsi-, contra-, and bilateral stimulation with the preferred stimulus were differentiated. Additionally, viewing conditions were varied between subjects to manipulate the degree of semantic processing necessary. For the semantic matching task, information from both visual hemifields is necessary to answer correctly.

For the VWFA, hemifield-independence has been demonstrated: The left-hemispheric VWFA is equally activated for words presented in the right and left visual fields (Cohen et al., 2000; Reinholz & Pollmann, 2005²). PPAs, in contrast, can be identified bilaterally (Epstein et al., 1999; Haxby et al., 1999; Ishai et al., 2000; Gorno-Tempini & Price, 2001; Reinholz & Pollmann, 2005). Activation of the PPAs is usually induced by foveal presentation of pictures of buildings, and visual hemifield effects are unknown to my knowledge. In the first fMRI-experiment (see Chapter 4), an increase in activation was observed for bilateral stimulation with redundant information in a category-detection task for pictures of faces and

² Reinholz & Pollmann, 2005 are the published results of Experiment 2

buildings. In this experiment, bilateral picture presentation will be compared to picture-word trials, i.e. trials with the same categorical information in both visual hemifields, but in a different format (word vs. picture). While identification of only one relevant stimulus was sufficient for the category-detection task in the first fMRI-experiment, information from both visual hemifields need to be integrated in the semantic matching task of this experiment. Therefore, possible stronger responses to bilateral stimulation in this experiment do not reflect the classical redundancy effect observed in the detection paradigm, but could also be obtained as more general response property of the PPAs.

In this paradigm, a stimulus of one format (i.e. a picture or a word) is presented in combination with either a stimulus from the same or from the other format in the contralateral visual hemifield. The following conclusions can be drawn from the comparison of bilateral redundant picture presentation with responses to mixed picture-word conditions: If written names of buildings elicit similar responses in the PPAs than the pictures themselves, no differences should be obtained in the contrast of picture-only conditions with mixed picture-word conditions. If, on the other hand, pictures of buildings elicit stronger activation than the words naming those pictures in the PPAs, higher activation should be observed for picture-only conditions contrasted with mixed picture-word conditions. In this case, further discrimination can be made between contra- and ipsilateral input: If signal changes in the PPAs are driven only by contralateral input, higher activation to bilateral stimulation with pictures should only be observed in the hemisphere receiving contralateral pictorial compared to written word input. If, however, signal changes in the PPAs depend on ipsilateral input as well, higher activation for bilateral picture stimulation should be observed

in both hemispheres. In the second fMRI-Experiment (see Chapter 5; Reinholz & Pollmann, 2005), no differences were obtained for words naming buildings and faces in the PPAs during passive viewing. In this experiment, possible effects of ‘deeper’ semantic processing will be investigated in a semantic matching task, where a comparison of pictures and their names was explicitly needed. Half of the participants had to perform the semantic matching task on the pictures and words, while the other half was instructed to attend to the same words and pictures but to perform a distractor discrimination task instead, comparable to the passive viewing conditions of Experiment 2. In addition to potential task-dependent effects of words on PPA activation, the more demanding semantic matching task will probably lead to attentional enhancement in the object-selective areas during picture presentations (e.g. O’Craven et al., 1999; Tong et al., 1998).

8.2 Materials and Methods

8.2.1 Participants

Twenty-one volunteers participated in this study (11 males). The data of one (male) subject had to be excluded because of poor fMRI data quality. Ten participants, of the remaining twenty subjects, performed the matching task and ten performed the passive viewing task. All subjects were consistent right handers according to their score in the Edinburgh Handedness Inventory (Oldfield, 1971). Subjects age was in the range of 22 to 30 years, with a mean age of 26 years. All subjects were native speakers of German and had no history of neurological or psychiatric disease. All subjects gave informed written consent according to the guidelines of the Max-

Planck-Institute. The fMRI-procedures were approved by the University of Leipzig ethics committee.

8.2.2 Stimuli and Procedures

Half of the subjects were carrying out the semantic matching task of Experiment A, i.e. they were instructed to make a forced choice about whether the two stimuli presented together belonged to the same subgroup of building type (i.e. church, castle, etc.), independent of the stimulus modality (picture or word). The other half of the subjects were instructed to attend to the picture and word stimuli but to perform a two-choice discrimination task instead (passive viewing task): Landolt-like rings with gaps on either top or bottom were presented simultaneously in the left and right visual hemifield and subjects had to decide as fast as possible whether the openings were in matching directions (both up or down) or mismatching directions (one pointing up and the other one down). The same passive viewing condition with this distractor task was used in the fMRI Experiment 2 (see Chapter 6). The effects of word-picture and picture-word presentation for the semantic matching task will be reported in the next chapter under the viewpoint of hemispheric specialization and interaction.

All scans were performed in a single session with an absolute scanning time of about 40 minutes for the semantic matching and 35 minutes for the passive viewing task. Stimuli were presented through LCD goggles (VisuaStim XGA, Resonance Technology), with a virtual distance of 120 cm. A fixation cross was visible throughout the entire experimental block. For each trial two stimuli were presented for 300 ms simultaneously in the LVF and RVF followed by an intertrial interval of 700 ms during which only the fixation cross was visible. Pictures and words in the LVF were combined with

pictures and words in the RVF, resulting in four presentation conditions: picture-picture, word-picture, picture-word, and word-word referring to the left-right ordering of the stimuli. Half of the trials were match and half mismatch trials. For match trials, two pictures were presented, each showing a different exemplar of the same subcategory of buildings (e.g. two pictures of different churches). For the two picture-word combinations, a picture was shown in one visual hemifield and the respective name was shown in the opposite visual hemifield. For word-word conditions, the same word was shown once in uppercase and once in lowercase in the LVF and RVF. Each stimulus (i.e. each picture and word) was shown equally often during match and mismatch trials and in each condition. In the passive viewing task, trials were included where words and pictures were shown with a scrambled picture in the opposite visual field. Pictures and words subtended about 6.9° of visual angle. The Landolt-like target circles in the passive viewing task were presented in black on a white square of the same size and had a size of about 1.8° visual angle themselves. All stimuli were presented with their center located 5.3° to the right or left of fixation. Critical trials were embedded in sequences of scrambled stimuli. These 'filler' baseline trials were introduced to reduce the overlap of the BOLD-responses elicited by critical trials. In a previous study, it was demonstrated that BOLD signal changes related to the critical trials obtained in this way are as large as the difference between critical and baseline trials presented in isolation (Pollmann et al., 2000). The sequences of scrambled images ranged from 5 to 9 trials with the same mean and standard deviation of length for all conditions: on average each critical event was preceded and followed by seven trials of scrambled pictures. The critical condition was never repeated in the successive trial. The transition probabilities were balanced. There

were no more than three consecutive repetitions of a single factor (e.g. no more than three word-word trials or three match trials). For the passive viewing experiment, on average, every 10th trial (including scrambled 'filler' trials) was a target trial, with match and no-match trials randomly selected. Critical trials were never directly succeeded or followed by target trials, there was at least one scrambled 'filler' trial in between. While the intervals between target and critical trials varied from two to eight seconds, the average interval between critical and target stimuli was the same for all conditions. By rotating conditions, four different sequences of the experimental phase were obtained that were balanced between subjects. During the course of the experiment, five null-events occurred where only the fixation cross was visible. Balanced across the two tasks, half of the subjects responded with the left hand first, and half with the right hand first. The index finger was associated to match-responses and the middle finger to mismatch-responses for both hands and for both tasks. Reaction times were afterwards corrected for hardware debouncing delays subtracting a key-specific constant based on inhouse measurements of about 40ms.

The importance of keeping the cross fixated all the time was explicitly stressed. Eye movements were monitored online with a video camera by the experimenter. Trials in which a saccade occurred were marked by the experimenter and excluded from analysis. This happened in less than 1% of the critical trials.

At the beginning of the experiment, subjects were shown successively all categories of buildings, i.e. the two corresponding pictures and the appropriate subcategory name. Subjects practiced the task in- and outside the scanner. This data that was not included in any analysis. After the experiment and outside the scanner, subjects filled out a short questionnaire and were debriefed.

8.2.3 fMRI procedure

In four participants with larger heads, the FOV was set to 22.4 cm. Baseline drifts of the signal were removed by temporal highpass filtering with a cut-off frequency of 1/50 Hz. In the spatial domain, a Gaussian filter with 7 mm FWHM was applied.

The relevant areas of object-selective processing were defined as a priori ROIs and voxels in these with a Z score greater than 3.09 ($p < 0.001$, uncorrected) were considered. All voxels outside these regions were significant at $p < 0.0001$ uncorrected ($Z > 3.72$).

For the time course analyses, as in Experiment 2, PPAs were identified from individual z -maps of bilateral picture presentation against baseline. The extraction of the time courses and calculation of the grand averages of the mean (Figure 7.2) was done in the same way as in Experiment 2 (see Chapter 6.2.3, p. 65).

8.3 Results

8.3.1 Behavioral Results

The behavioral effects in the semantic matching task and their neural correlates will be reported in the next chapter together with the effects related to word-picture and picture-word matching. For the aspects investigated in this chapter, it is sufficient to report that subjects were able to perform satisfactorily in both tasks with a mean of 93.3% and 72.5% correct answers, respectively, for the passive viewing and semantic matching task. Only correct answers were considered in the contrasts reported.

8.3.2 Imaging Results

Effects of Visual Field in Picture-Word Combinations

To determine activation elicited by contra- and ipsilateral presentation of the relevant stimulus, contrasts of word-picture and picture-word trials were calculated against the baseline of scrambled images. Since there were no significant differences in the ROIs in the contrast of match against mismatch trials, both matching conditions were collapsed to one condition. As can be seen (Fig. 7.2), the three relevant ROIs (LH PPA, RH PPA, and VWFA) were activated in both conditions at almost identical locations. For the LH PPA the respective coordinates are: $-26x -48y -6z$ (word-picture) and $-26x -50y -6z$ (picture-word); for the RH PPA: $25x -47y -5z$ (word-picture) and $28x -47 -6z$ (picture-word), and for the VWFA: $-41x -57y -8z$ (word-picture) and $-41x -54y -9z$ (picture-word).

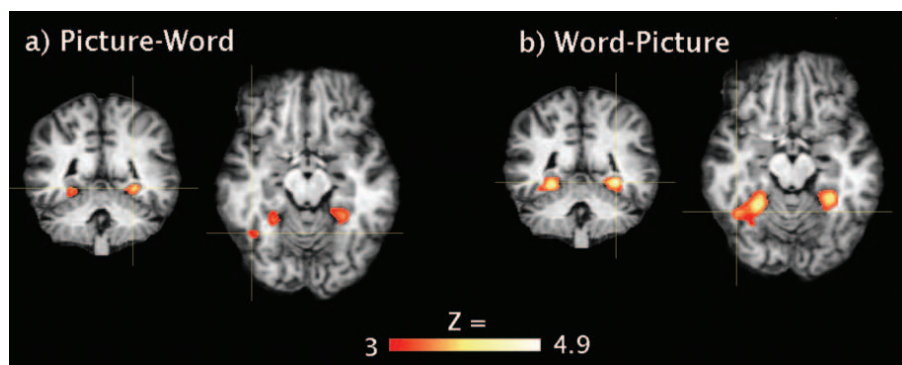


Figure 8.1 Group activation for the contrast for word-picture and picture-word conditions against scrambled pictures. Left hemisphere is on the left. Pictures and words activate the PPAs bilaterally and a left-lateralized VWFA. The colorscale indicates Z-scores.

Effects of Contralateral Stimulation in VWFA and PPAs

Conditions with picture-word and word-picture presentations were subtracted from conditions with bilateral redundant presentations of words and pictures, respectively. No significant differences were found in the contrasts of match against mismatch trials for bilateral word and picture conditions at any of the ROIs and were therefore collapsed to one bilateral picture and one bilateral word condition.

For pictures (Fig. 7.3), bilateral picture presentation led to higher activation in the left hemispheric PPA contrasted with picture-word (at -26x -50y 0z) as well as word-picture (at -26x -47y 0z) conditions, i.e. the left hemispheric PPA responded more strongly when a picture was presented instead of a word in the contralateral and ipsilateral visual hemifield alike. For the right hemispheric PPA, there was no significant activation in these contrasts at the $p=0.001$ threshold. Lowering the threshold to $p=0.005$, peaks of activation comparable to the location of the PPA were found at 28x -41y -11z and at 28x -38y -9z, respectively, indicating the same pattern of stronger responses to bilateral picture presentation than to picture-word and to word-picture conditions.

For words (Fig. 7.3), both conditions with mixed word-picture conditions (i.e. word-picture and picture-word) led to higher activation in the PPAs bilaterally than word-word presentations but no differences were observed for the VWFA, not even at the lower threshold. Bilateral redundant word conditions did result in significant left-lateralized VWFA activation (-38x -68y -8z), as is evident in the contrast against baseline.

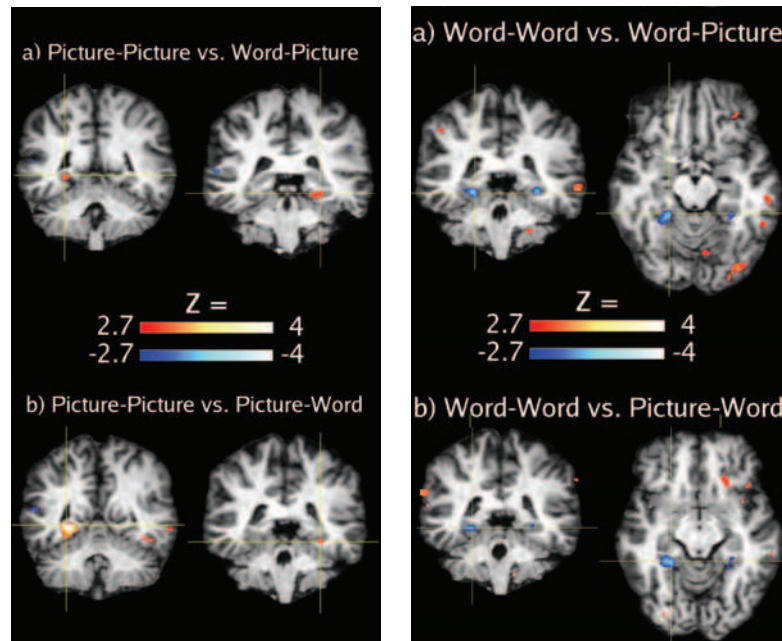


Figure 8.2 Group activation for the contrast for matching picture-picture and word-word conditions against word-picture and picture-word conditions, respectively. Trials are collapsed across both task conditions. Pictures and words activate the PPAs bilaterally and a left-lateralized VWFA. The colorscale indicates Z-scores with the redish scale indicating activation for bilateral redundant conditions, and with the blueish scale indicating stronger activations to mixed picture-word combinations.

Task effect

In the discussion of Experiment 2 in the previous chapter, it was hypothesized that semantic matching of words might lead to higher activation in the object-related areas than passive viewing via top-down processing induced by words. ANOVAs on the individual percent signal changes of PPA activation were conducted with Time (timepoints 0 to 10), Task (passive viewing, semantic matching), Condition (word-word, picture-picture) and Hemisphere (LH, RH) as factors. There were significant main effects of Time [$F_{(11,99)}=17.81$; $p<0.05$] and Condition [$F_{(11,99)}=60.38$; $p<0.05$], along with a significant interaction between Task and Condition [$F_{(1,9)}=11.35$;

$p < 0.05$], but no significant main effects of Task or Hemisphere. As can be seen in Figure 7.4, the main effect of Condition is based on generally higher activation for pictures than words in both hemispheres and tasks, while the interaction is based on greater differences in signal change for pictures compared to words under semantic matching (0.6% vs. 0.3% maximum signal change for pictures and words) than under passive viewing conditions (0.3% vs. 0.1% maximum signal change).

To determine whether word-picture and picture-picture trials lead to similar activation in the PPAs for the semantic matching, but not for the passive viewing task, two separate ANOVAs were performed. Factors of both analyses were again Time (timepoints 0 to 10), Task (passive viewing, semantic matching), and Hemisphere (LH, RH) remained, but the Condition factor was tested separately in one analysis for word-picture and picture-picture trials (WP, PP), and in a second analysis for picture-word and picture-picture trials (PW, PP). In both analyses, there was only a main effect of Condition [$F_{(1,9)} = 8.33$; $p < 0.05$, and $F_{(1,9)} = 10.87$; $p < 0.05$]. There were no interactions between Condition and Task, or Condition, Task and Hemisphere. The main effect of condition is based on the effect of stronger signal changes for picture-picture than picture-word and word-picture stimulation, evident in the contrast images as well (Figure 7.2).

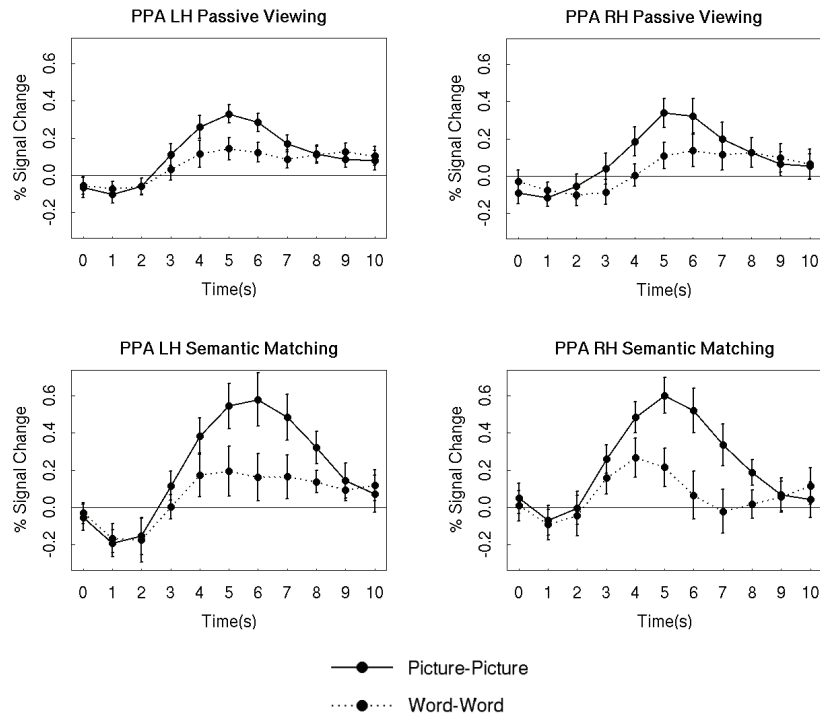


Figure 8.3 *Changes of the hemodynamic response to word- and picture-conditions for the left and right hemispheric PPA under conditions of passive viewing and semantic matching. Time courses are based on individual ROIs. Depicted are mean signal changes and standard-errors of the mean (see Methods).*

8.4 Discussion

This experiment investigated effects of lateralized and bilateral-redundant stimulus displays on BOLD signal changes in areas specifically engaged in processing words and pictures of buildings. Replicating numerous previous findings (e.g. Cohen et al., 2000, 2002; Gorno-Tempini & Price, 2001; Haxby et al., 1999; Ishai et al., 2000; O'Craven & Kanwisher, 2000) including the results from the first and second experiment, areas in the parahippocampal gyrus most strongly responded to pictures of buildings while a left-

lateralized area in the lateral occipital sulcus responded most strongly to written words. This pattern of bilateral PPA activation and left-lateralized activation of the VWFA was found in both picture-word combinations when tested against baseline, i.e. independent of the visual field of the preferred stimulus. The observed hemifield independence of VWFA activation is consistent with previous reports of functional imaging studies (Cohen et al., 2000, 2002; Reinholz & Pollmann, 2005).

The hemifield-independence of PPA activation is consistent with findings that high-level visual areas are generally non-retinotopic (Grill-Spector et al., 1998; Tootell et al., 1998). Recently, however, it has been suggested that some degree of retinotopy exists even in high-level visual areas: the sensitivity to eccentricity (Levy et al., 2001, 2004; Malach et al., 2002; Grill-Spector & Malach, 2004). In this experiment, modulation of PPA responses due to periphery effects should be the same across conditions and cannot account for any visual field effects, because pictures were always presented in the LVF and RVF with the same distance from the fixation point.

It may be argued that bilateral PPA activation in the word-picture and picture-word conditions might reflect a response to the contralaterally presented word instead of a response to the ipsilateral picture. This, however, is unlikely. Firstly, there was no evidence for words eliciting substantial activations in the PPAs in the time course analyses for bilateral word presentation. Secondly, although any influences of the word stimuli in the mixed conditions cannot be ruled out completely, the stronger responses of the PPAs to bilateral redundant picture presentations compared to mixed picture-word presentations show that pictures of buildings lead at least to significantly greater signal changes than the names of buildings.

An increase in ipsilateral activation during unilateral stimulation can also indicate hemispheric resource sharing (Pollmann et al., 2003). In this case, homologous areas in the ipsilateral hemisphere are recruited during unilateral input when the contralateral hemisphere reaches its input limit. The possibility that effects of hemispheric resource sharing might account in part for the bilateral activation of the object selective areas during unilateral input can not completely be eliminated. However, the observed additivity for bilateral picture presentation cannot be explained solely by hemispheric resource sharing processes, because one would not expect higher activation to bilateral than to unilateral presentation in both hemisphere, when the contralateral PPA has already reached its resource limit for the contralateral input.

The increase in activation for bilateral picture presentation was not restricted to the hemisphere directly receiving picture compared to word stimulation from the contralateral visual hemifield. This finding indicates that presentation of a preferred stimulus in the ipsilateral visual field can increase PPA activation. Further evidence that input of ipsi- and contralateral visual fields can have additive effects on activation of extrastriate visual areas comes from paradigms investigating the redundant target effect. Faster responses to two targets presented bilaterally compared to unilateral presentation of a single target were accompanied by shorter latencies in early components of the visual ERPs (Miniussi et al., 1998; deGelder et al., 2001) and enhanced activation in extrastriate cortex in a patient with callosal agenesis (Iacoboni et al., 2000).

In the first experiment, a comparable summation effect in the PPAs was obtained when bilateral redundant picture presentation was contrasted to combination with pictures of faces (see Chapter 5.3.2, page 40). The replication of this effect for different tasks and

stimulus combinations indicates that neural summation in the PPAs generalizes across different paradigms (see Chapter 10 for an additional discussion).

The observed effects of task demands in the PPAs with higher signal changes for pictures of buildings under the more demanding semantic matching condition most likely reflects a main effect of attentional modulation. Analyzing the timecourses obtained from the individually defined PPAs during bilateral picture presentation, there was no interaction effect of task demands with the conditions of bilateral or unilateral picture presentation. In the semantic matching task, attention probably modulates object-selective areas tonically and phasically because of overall task demands (Avidan et al., 2003; Lueschow et al., 2004; O'Craven et al., 1999; Serences et al., 2004) and specific working memory processes (Ranganath et al., 2004a, 2004b).

For the VWFA, activation was found in both picture-word conditions, i.e. when words were presented in the right as well as left visual hemifield, and in bilateral word-word conditions, but no significant differences were observed for picture-word or word-picture conditions in the comparison to the word-word conditions. To my knowledge, there are no imaging studies investigating effects of bilateral word matching in areas specifically involved in visual word processing. Behavioral studies of bilateral word presentation have mostly focussed on faster reactions to bilateral redundant word presentation compared to unilateral presentation of single words in lexical decision tasks (Mohr et al., 1994, 1996; Zaidel & Rayman, 1994).

Taken together, the results of this experiment show that the PPAs and the VWFA both show hemifield independent activation for input in the ipsi- and contralateral visual hemifield. Simultaneous

stimulation in both visual hemifields can contribute additively to the PPA activation. No additive effects were observed for the VWFA. These findings suggests that differences in activation patterns to bilateral redundant stimulation might be an additional characteristic for high level visual areas in addition to lateralization and selectivity for certain stimulus formats or categories.

8.5 Conclusion

In conclusion, the observed activation differences between ipsi-, contra- and bilateral input suggest that both visual hemifields are represented in the PPAs with input mechanisms that can show additive effects. Furthermore, the observation of stronger activation in both hemispheres, albeit weaker in the right hemisphere, to redundant than to mixed picture-word conditions revealed that the response of the PPA for words naming pictures is smaller than the response to the pictures themselves. This was further demonstrated by an analysis of the hemodynamic response in the PPAs for bilateral word presentation under passive viewing and semantic matching tasks.

While the latter effect replicates the negligible effect of written category names during the passive viewing of lateralized pictures and names of faces and buildings obtained in the second experiment, the increase in activation for bilateral stimulation extends the findings of the first experiment to a different task and different source of divergent information (i.e. format instead of category).

9 Experiment 3 – Effects of Hemispheric Specialization

9.1 Introduction

This experiment reports the effects of the semantic matching task, especially with respect to possible effects of hemispheric specialization in visual word form processing.

In lexical decision tasks, where a briefly presented stimulus has to be classified as word or non-word, an RVF advantage for visual word recognition is commonly reported indicating a left hemispheric specialization for visual word processing (see Chiarello, 1988; and Querné et al., 2000 for overviews). In Chapter 2.4.2 lateralization effects of visual word processing have been discussed in more detail.

It has been suggested that different hemispheric competences for the pre-lexical visual processing of written words extends to lateralization effects on lexical tasks. The present experiment aimed at investigating whether hemispheric differences can also be obtained in an even more demanding semantic matching task for words presented in the LVF and RVF. Furthermore, possible behavioral effects on decision latencies and accuracy can be related to the functional imaging data, i.e. to test whether lateralized activation differences correspond to the respective visual hemifield advantages.

According to a behavioral RVF advantage, word-specific activation in the left hemisphere has been observed during

processing of centrally presented written words in functional imaging (e.g. Puce et al., 1996; Hagoort et al., 1999; Polk et al., 2002) as well as in electrophysiological studies (e.g. Khateb et al., 2001; Tarkiainen et al., 2002; Rossion et al., 2003b). Left-lateralized VWFA activation for words specifically presented in the ipsilateral LVF and contralateral RVF (Cohen et al., 2000; Reinholz & Pollmann, 2005) further indicates left-hemispheric specialization in visual word form processing.

In contrast, no differences have been reported in recognition and semantic categorization of pictures of objects when presented in the left or right visual hemifield in most studies (Biederman & Cooper, 1991; Koivisto, 2000; Koivisto & Revonsuo, 2003a; Levine & Banich, 1982, but see Koivisto & Revonsuo, 2003b and McAuliffe & Knowlton, 2001). In accordance with the absence of lateralization effects in the behavioral data, activation in areas related to object recognition is typically observed bilaterally (e.g. Grill-Spector et al., 1998; Malach et al., 1995; but see Niemeier et al., 2005 for a relative effect of visual hemifield, see Chapter 2.4.1).

Effects of visual hemifield on activation differences in the PPAs have so far not been investigated, although a higher responsiveness towards peripheral stimulation was observed (Levy et al., 2004). In the second experiment, responses to pictures of buildings were less pronounced in the right hemisphere, but no activation differences were obtained in the analysis of the hemodynamic response within the right hemispheric PPA.

Any visual field advantages for picture-word combinations therefore most likely reflect differences in visual word processing. An expected RVF advantage for word presentation during semantic matching of word-picture combinations was evident in behavioral studies, although sometimes this difference was not statistically

significant (Pellegrino et al., 1977; Harris et al., 1977; Koivisto & Revonsuo, 2003a).

Different models of hemispheric interaction related to the RVF advantage in word recognition have been proposed. To differentiate between interhemispheric interaction patterns based on callosal relay versus direct access, reaction time differences can be analyzed. One criterion for a direct access mode of processing is a response hand by visual field interaction (see Chapter 3.4).

In behavioral studies of hemispheric specialization and interaction, conditions of bilateral redundant presentation are often compared to unilateral presentation in order to detect hemispheric dominance when information is presented to both hemispheres simultaneously (e.g. Hellige et al., 1988; 1989). In this experiment, stimuli are always presented bilaterally, i.e. there is no within-hemisphere manipulation. This paradigm removes the confound of hemispheric load differences between uni- and bilateral presentations (Banich & Shenker, 1994) and ensures that both stimuli are processed, but generalizations to other paradigms might be limited. Still, activation differences in the anterior cingulate cortex could indicate differences in hemispheric control (Stephan et al., 2003) or interhemispheric information transfer (Pollmann et al., 2003).

The analysis of the behavioral and functional imaging data of this experiment examines whether the semantic subcategory decision is made faster or more accurate if the word is presented in the RVF than in the LVF (i.e. contralateral to the specialized hemisphere) and if so, whether this effect is related to or independent of activation changes in the VWFA or PPAs. Activation changes in the VWFA and PPAs could identify patterns of hemispheric interaction at the stages of category-specific visual processing of pictures and words.

9.2 Materials and Methods

9.2.1 Participants

Ten volunteers participated in this study (5 males). All subjects were consistent right handers according to their score in the Edinburgh Handedness Inventory (Oldfield, 1971). Subjects age was in the range of 23 to 29 years, with a mean age of about 26 years. All subjects were native speakers of German and had no history of neurological or psychiatric disease. All subjects gave informed written consent according to the guidelines of the Max-Planck-Institute. The fMRI procedures were approved by the University of Leipzig ethics committee.

9.2.2 Stimuli and Procedures

Stimuli and procedures are described in the previous chapter. Figure 8.1 shows the semantic matching task again with its main parameters. Subjects had to decide, whether the two stimuli belonged to same type of building, irrespective of the presentation format, i.e. if the building-type was shown as word or picture. The inter-trial-interval was filled with scramble trials, ranging from 5 to 9 repetitions with a mean interval of 7 scrambled trials. Response hand was switched according to an A-B-B-A schema, with the beginning hand balanced between subjects.

The fMRI procedure is described in the previous chapter. All analyses are based only on the data of subjects in the group of the semantic matching task. Only correct responses were considered for the functional imaging contrasts.

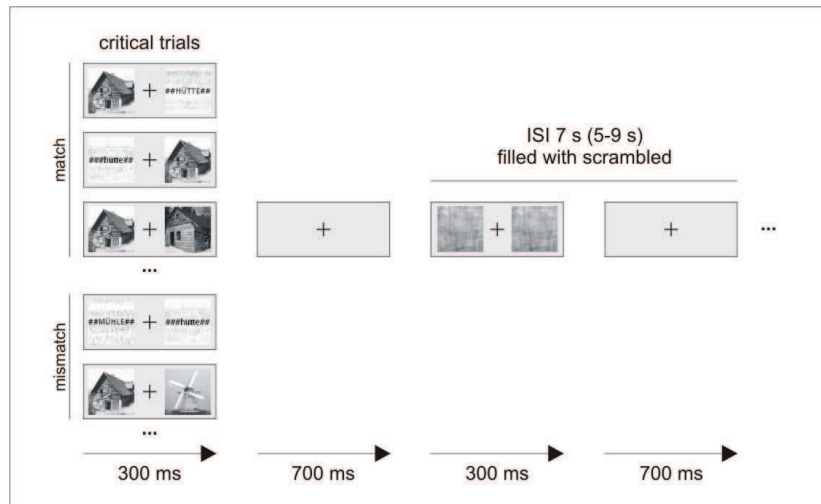


Figure 9.1. *Semantic matching task. On each trial, a picture or a word was presented in the LVF or RVF with a different picture or word in the opposite visual hemifield. Subjects had to decide as quickly and as accurate as possible, whether the two stimuli were the same subtype of building.*

9.3 Results

9.3.1 Behavioral Results

Repeated measures ANOVAs with the factors Response (match, mismatch) and Condition (word-picture, picture-word) with percent accuracy and mean reaction times on correct trials as dependent variables were calculated.

For reaction times of correct matching and mismatching trials, they were significant main effects of Condition [$F_{(1,9)}=5.9$; $p<0.05$] and Response [$F_{(1,9)}=17.54$; $p<0.05$], but no significant interaction between those two. Paired t-tests on averaged matching and mismatching trials, showed that decision latencies were shorter when the word was presented in the RVF (1339ms) than in the LVF (1415ms, $T_9=2.72$; $p<0.01$).

For percent accuracy, there was a main effect of Condition [$F_{(1,9)}=13.82$; $p<0.05$], and a main effect of Response [$F_{(1,9)}=7.07$; $p<0.05$] but no interaction between the two factors. Therefore, accuracy was averaged across match and mismatch trials and compared between the two conditions. Accuracy was higher in response to words displayed in the RVF (73.5 %) than to words in the LVF (64.5%, $T_9=3.72$; $p<0.01$, Fig. 8.2).

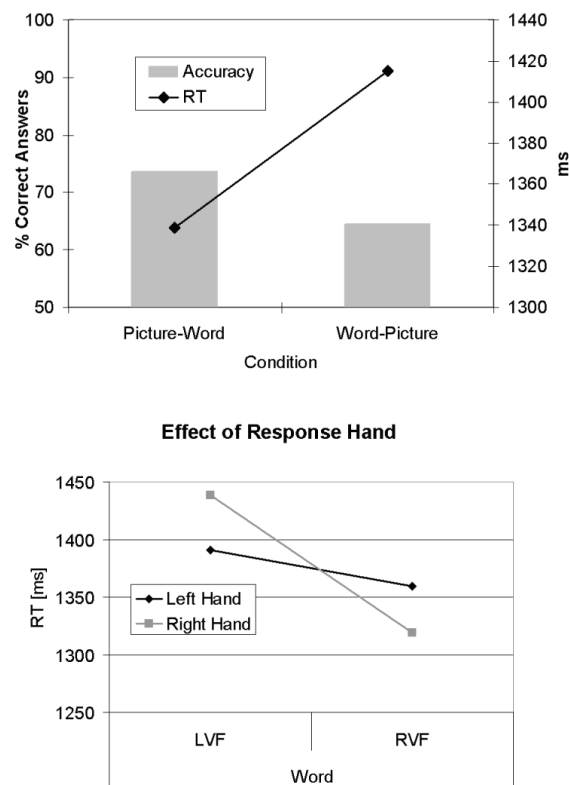


Figure 9.2 *Top: Overall reaction times and accuracy data for picture-word and word-picture trials averaged across match and mismatching conditions. Bottom: Illustration of response hand by visual field interaction for the decision latencies with the hand ipsilateral to the visual hemifield of word presentation always being faster.*

To investigate effects of response hand, a repeated measures ANOVA was conducted with the factors Response Hand (left, right) and Visual Field (word-picture, picture-word) on the reaction time data. Along with the reported main effect of Visual Field [$F_{(1,9)}=6.73$; $p<0.05$], there was a significant Response Hand by Visual Field interaction [$F_{(1,9)}=7.06$; $p<0.05$]. As can be seen in Figure 8.2, reaction times were faster for the Response Hand ipsilateral to the visual hemifield of word presentation. For the accuracy data, there was a main effect of Response Hand [$F_{(1,9)}=5.85$; $p<0.05$] along with the main effect of Visual Field [$F_{(1,9)}=15.241$; $p<0.05$], but no interaction between those two. Response with the right hand were more accurate (71.4%) than responses with the left hand (66.6%).

9.3.2 Imaging Results

To determine activation elicited by each condition, both contrasts of match and mismatch word-picture and match and mismatch picture-word trials were calculated against the baseline of scrambled images. As can be seen (Fig. 8.3), the three relevant ROIs (LH PPA, RH PPA, and VWFA) were significantly activated in both conditions at almost identical locations. For the LH PPA the respective coordinates were: -26x -50y -6z (word-picture) and -26x -48y -6z (picture-word); for the RH PPA: 25x -47y -6z (word-picture) and 25x -47 -6z (picture-word), and for the VWFA: -47x -53y -9z (word-picture) and -47x -56y -6z (picture-word). Comparing the locations of the relevant ROIs with the coordinates collapsed across both task conditions (see previous chapter), the results were very similar.

In the direct contrast of word-picture against picture-word conditions, there were no significant differences at the location of the PPAs or the left-hemispheric VWFA. In the whole brain analysis, no significant difference elsewhere in the brain was observed. Due to

the behavioral evidence of a direct access effect, possible activation differences at the right hemispheric area symmetric to the left hemispheric VWFA were specifically investigated. The threshold was adjusted to the $p < 0.001$ level at the corresponding location of the right hemisphere. There was a significant peak of activation at the right lateral occipital sulcus at 46x -59y -6z (VWFA locations: -47x -53y -9z, and -47x -56y -6z), indicating higher activation when the word was presented in the contra- than in the ipsilateral visual hemifield. This activation peak reached significance at the $p < 0.0001$ level, when averaging across the eight of the ten subjects, who actually showed the behavioral effect of the direct access pattern, i.e. faster reactions with the left than with the right hand for words presented in the LVF.

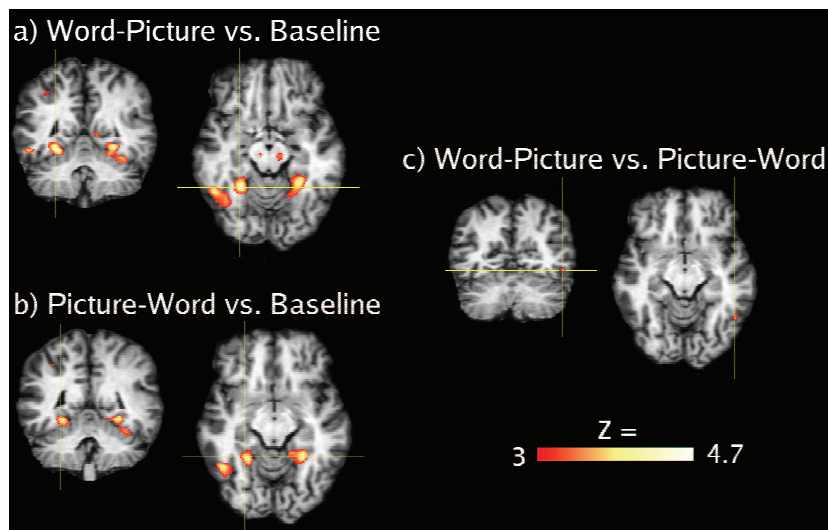


Figure 9.3 Top (a): Group activations for the contrast of word-picture conditions against the baseline of scrambled images. Cross-hairs indicate the location of the left hemispheric PPA. Colorscales indicate z-scores. Bottom (b): Group activations for the contrast of picture-word conditions against the baseline of scrambled images. Cross-hairs again indicate the location of the left hemispheric PPA. Right (c): Direct contrast of word-picture against picture-word conditions. Cross-hairs indicate the right hemispheric activation (46x -59y -6z) at a location almost symmetrical to the left hemispheric VWFA (-47x -53y -9z and -47x -56y -6z, respectively).

To determine brain areas involved in both conditions, it was analysed which voxels were significantly activated ($p < 0.0001$) in both the word-picture and the picture-word contrast if tested against baseline, respectively. Along with a lateral prefrontal activation ($-44x$ $18y$ $21z$), clusters of activation were found at the left insula ($-32x$ $15y$ $3z$) and at the left cingulate sulcus ($-2x$ $16y$ $44z$; Fig. 8.4).

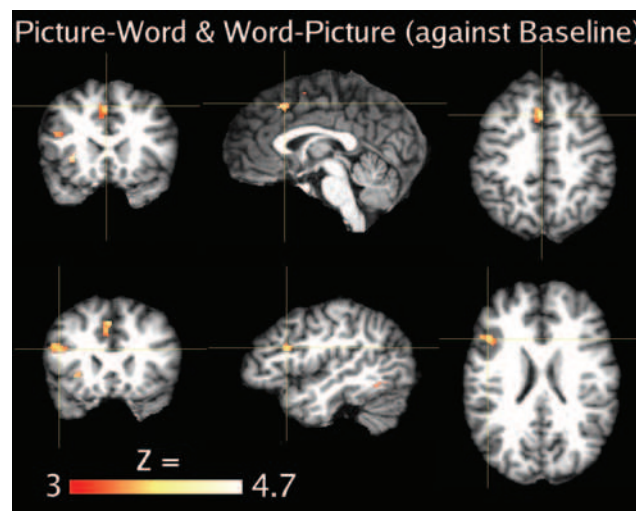


Figure 9.4 Consistent activation in both word-picture and picture-word trials, i.e. overlap of significantly ($p < 0.0001$) activated voxels in the contrast of each condition against their baselines. Colorscales indicate z-scores.

9.4 Discussion

Responses were more accurate and decision latencies shorter when the word was presented in the RVF and the picture in the LVF than in the opposite case. The same trend was observed in other behavioral studies using similar paradigms (Harris et al., 1997; Koivisto & Revonsuo, 2003a; Pellegrino et al., 1977) demonstrating that a RVF advantage for word recognition often observed in lexical decision tasks extends to more demanding tasks and stimulation conditions.

The main effect of a RVF advantage for word presentation went along with a left-lateralized activation for both picture-word conditions at the location of the VWFA, further indicating that the left hemisphere is specialized in visual word processing. Words from both visual fields elicited activation in the left hemisphere; i.e. information from the ipsilateral visual hemifield was ultimately transferred across the hemispheres (Khateb et al., 2001). While this has been demonstrated for unilateral presentation of words before (Cohen et al., 2000; Reinholz & Pollmann, 2005), these results show that the hemifield independent left-lateralized activation can be observed during stimulation with pictures in the contralateral field and for more complex tasks.

The main effect in response time for words in the RVF was modulated by a visual field by response hand interaction: responses were faster with the hand ipsilateral to the words' visual field compared to responses with the contralateral hand. This pattern is usually taken as evidence for direct access models (e.g. Iacoboni & Zaidel, 1996) where information is processed directly in the hemisphere of input. Direct access pattern of word processing have also been reported in lexical decision tasks for behavioral (Iacoboni & Zaidel, 1996) and electrophysiological measures (Schweinberger et al., 1994, but see Khateb et al., 2001). Supporting evidence that some word processing was carried out in the right hemisphere comes from the finding of a stronger right-hemispheric activation for word-picture than picture-word combinations at a location almost symmetrical to the left-hemispheric VWFA. It has been suggested that a right homologue of the VWFA can engage in visual word processing by carrying out letter identification or 'graphemic descriptions' (Cohen et al., 2003; Molko et al., 2002). This functional homologous area, however, is supposedly located at V4 (e.g.

McCandliss et al., 2003), i.e. at a different location (McKeefry & Zeki, 1997) than the activation peak observed in this experiment. Right hemispheric activation at similar locations has been reported in a functional imaging study of a patient suffering from pure alexia, a neuropsychological deficit where patients are unaffected in their writing and spelling abilities, but have a specific reading deficit (Cohen et al., 2003; 2004b). Their residual ability to name written words through a typical strategy of letter-by-letter identification indicates that the right hemisphere is generally able to process visual words, although less efficiently. In this experiment, words presented in the LVF were probably not processed exclusively in the right hemisphere, a strong left-hemispheric VWFA activation was nevertheless observed for the test for word-picture conditions against baseline, but with a stronger degree of right lateralization. A shift in lateralization from bilateral towards left-lateralized VWFA activation has been demonstrated for word compared to non-word reading in healthy individuals (Tagamets et al., 2000), suggesting that bilateral areas related to processing of alphabetical material can interact across the hemispheres (Vigneau et al., 2005). For the current experiment, is possible that on some word-picture trials a matching decision could be made based on information from a characteristic string of letters, for example for words containing umlauts. A visual analysis that could have been carried out in the right hemisphere during the direct access of information from the contralateral visual hemifield.

Areas specifically involved in picture processing, i.e. the PPAs, were bilaterally activated for pictures of buildings presented in the LVF and RVF, further supporting that the behavioral effects observed in this experiment are due to lateralization of word rather than picture processing. There were no activation differences in the

right or left hemispheric PPA comparing contra- with ipsilateral stimulation, which is congruent with the supposedly general non-retinotopic nature of object-selective areas (Grill-Spector et al., 1998; Halgren et al., 1999; Tootell et al., 1998, but see Niemeier et al., 2005).

There was no evidence for any other hemispheric activation differences between word-picture and picture-word conditions as indicator for condition-specific areas involved in performing the task. Instead, the left-lateralized activation of prefrontal and cingulate regions independent of stimulation suggests that control processes might have been similar for both conditions (Stephan et al., 2003). Left-hemispheric lateral frontal activation in this paradigm could reflect working memory processes. It is possible, that working memory processes under these cross-format task conditions reflect the comparison of conceptual information extracted from the pictures and words in their respective visual areas. It remains unclear whether the maintained information in this case is of semantic (Fletcher & Henson, 2001; Mecklinger et al., 2000; Shivde & Thompson-Schill, 2004) or visual nature (Druzgal & D'Esposito 2001, 2003; Ranganath et al., 2004b; Serences et al., 2004). The activation could also reflect more abstract processes of selecting task-relevant information, for example in the general context of scrambled trials and trials requiring a matching response (e.g. Brass & von Cramon, 2004). Similar activation of left dorsolateral cortex was found when pictures had to be compared with words at the semantic level in a one-back matching task (Sevastianov et al., 2002).

There were no activation peaks in the left inferior temporal cortex or at temporo-polar regions, which have been associated to format-independent semantic processing for pictures as well as words

(Bookheimer et al., 1995; Chee et al., 2000; Moore & Price, 1999; Bright et al., 2004). In these studies, areas commonly activated by semantic processing of pictures and words were mostly determined in contrasting pure word with pure picture conditions. It could be the case, that semantic processing of mixed picture-conditions required in this experiment leads to stronger involvement of the left inferior prefrontal cortex than anterior temporal cortices. Further functional imaging on similar paradigms is needed to clarify the role of anterior temporal/fusiform regions in this task, ideally with PET and fMRI (Devlin et al., 2000).

9.5 Conclusion

In conclusion, the results of this experiment demonstrated hemispheric specialization and interaction in behavioral measures that corresponded well to the functional imaging data of high-level visual areas. Semantic matching of pictures and words was more efficient when words were presented in the RVF than in the LVF. This behavioral RVF advantage was in accordance with a left hemispheric specialization for visual word form processing indicated by left-lateralized VWFA activation for both conditions. In addition, the reaction time data suggested a direct processing mode for words presented in the LVF, and a corresponding stronger activation in the right hemisphere was found at a location comparable to the VWFA for word-picture conditions. Activation of areas related to the picture processing (PPAs) was observed bilaterally for pictures presented in the LVF and RVF. The results suggest that both hemispheres are equally able in picture processing, but the left hemisphere is specialized in visual word form processing. Although most efficient in the left hemisphere, visual word processing is not restricted to the specialized hemisphere, but is partly accomplished via direct access

for words presented in the LVF in this paradigm of a semantic matching task.

10 General Discussion

The main aim of this dissertation was to investigate the responses of object-selective areas to contra-, ipsi- and bilateral stimulation with preferred and unpreferred stimuli to investigate hemispheric interaction at the level of object- and word-specific visual processing. In three fMRI experiments, selective activation for pictures of faces and buildings at locations in agreement to FFA and PPAs coordinates in the literature could be replicated (e.g. Aguirre et al., 1998a; Chao et al., 1999; Gauthier et al., 2000; Haxby et al., 1999; Ishai et al., 2000; Puce et al., 1996; Spiridon et al., 2006; Spiridon & Kanwisher, 2002; Tong et al., 2000; Xu, 2005). Similarly, word-specific activation was found left-lateralized in a region corresponding to the VWFA (e.g. Cohen et al., 2000a, 2000b; Cohen & Dehaene, 2004; Kronbichler et al., 2004; McCandliss et al., 2003; Pammer et al., 2004; Vigneau et al., 2005). Different responses of those areas were found for the different conditions of bi- and unilateral stimulation, which will now be discussed in the general context of hemispheric interaction, specialization, and control.

10.1 Response Properties of FFA, PPA, and VWFA

Different responses to variations of categorical input from the contra- and ipsilateral visual hemifield in the FFA and PPAs were demonstrated across different tasks, subjects, and slight variations in the experimental paradigms.

Object-selective areas are generally thought to be non-retinotopic, i.e. activated by contra- as well as ipsilateral stimulation (Grill-

Spector et al., 1998; Halgren et al., 1999; Tootell et al., 1998). Investigating the responses to presentation of preferred stimuli in the ipsi- or contralateral visual hemifield revealed no effect of visual hemifield in the analysis of hemodynamic responses to preferred pictures in the FFA and PPA in Experiment 2. Additionally, in Experiment 3, word-picture as well as picture-word conditions elicited bilateral PPA activation. These results suggest that the PPA and FFA respond about equally strong to preferred pictures in each visual hemifield for tasks of passive viewing, category detection, and semantic matching. Although a lateralization difference was observed for pictures of faces and FFA between the category detection and the passive viewing task.

It has been suggested that remaining effects of visual hemifield differences indicate the level of visual processing carried out in these visual areas. Accordingly, areas in the lateral-occipital complex still showing a relative preference for the contralateral visual hemifield evident in early visual areas have been classified as intermediate rather than high-level visual areas (Niemeier et al., 2005). The independence of visual hemifield presentation of the preferred stimulus on activation elicited in the PPA and FFA further supports the assumption that activation in object-selective areas is related to visual processing of pictures from the respective categories at high levels of abstraction.

For pictures of faces, right-lateralized processing has been found in ERP (Yovel et al., 2003) and MEG studies, (Halgren et al., 2000), where sometimes bilateral symmetric responses were observed (Liu et al., 2002). No differences between ipsi- and contralateral face presentation were observed in any of these studies. A relative increase in activation for peripheral stimulation with pictures of buildings has been reported (Levy et al., 2004), but visual hemifield

effects for pictures of buildings and PPA have to my knowledge not been specifically investigated before.

The increase in response to bilateral compared to unilateral input evident in Experiment 1 and 3 showed that responses of the FFA and PPA to preferred pictures dynamically depended on input from both visual hemifields and did not work in a simple all-or-nothing way. Even though comparable activation could be elicited by contra- and ipsilateral presentation with pictures of faces and buildings in the FFA and PPA, respectively, the presence of bilateral redundant compared to different categorical information in the opposite visual field lead to an increase in the FFA and PPA activation. Thus, even though the response was independent of the visual hemifield per se, input from both visual hemifields contributed to the activation of the FFA and PPA. The differential effects to input from the opposite visual hemifield indicated hemispheric interaction at this specific processing level and demonstrated that responses of object-selective areas are sensitive to the categorical information presented in combination with the preferred stimuli. This evidence is an important characteristic of these object-selective areas and adds new information on the response properties of the FFA and PPA currently known.

Although it was not the main focus of this dissertation to specifically investigate different models of FFA and PPA functionality with respect to more general aspects of object representation or processing, the observation of bilateral PPA responses during category detection and semantic matching demonstrated that pictures of building elicited specific activation at different levels of visual differentiation (i.e. category-based in Experiment 1, and subcategory-based in Experiment 3). Similar activation for the processing of specific types of buildings has been reported before

(Gorno-Tempini & Price, 2001). These results do not generally argue against an expertise hypothesis as underlying principle of object-specific activation patterns, however, they further support the idea that specific activation for the processing of pictures of buildings can be obtained consistently on a variety of different tasks and across different populations of subjects (Malach et al., 2002; Peelen & Downing, 2005; Spiridon et al., 2006).

To demonstrate and determine the effects of input from input of the opposite visual hemifield on activation of object-selective areas is also important, because lately the FFA and PPA have been investigated not only to determine their characteristic response properties, but also to investigate other cognitive models, e.g. related to attentional processes (e.g. Marois et al., 2004; O'Craven et al., 1999). Similarly, the response properties established in this series of experiments can also be used to investigate other effects of hemispheric interaction. For example, the effects of task difficulty on interhemispheric interaction (e.g. Belger & Banich, 1998; Maertens & Pollmann, 2005; Weissman & Banich, 2000).

10.1.1 Effects of Bilateral Redundant Stimulation

An increase in activation was found for bilateral redundant information compared to only unilateral presentation of preferred stimuli. This was observed for redundant compared to mixed categorical information in a category detection task (Experiment 1), and for redundant compared to mixed format information across passive viewing and semantic matching (Experiment 3).

This increase in activation was associated with a redundant targets effect for the reaction times in the category detection task. Responses were faster when two pictures of faces or two pictures of buildings were presented, compared to mixed face-building

conditions. In principle, reaction times to mixed face-building trials could have been generally faster, because they were always match trials, since the relevant category was either a face or a building. The prolongation of reaction times, however, indicates that subjects did not use a specific strategy, but support the assumption that an actual matching process was carried out. Generally, RTEs have been observed on a variety of different tasks and across different formats (e.g. Miller, 1982; Marks & Hellige, 2003; Mohr et al., 1996). While the redundancy effect is likely to occur at different stages for different paradigms and stimuli (Minussi et al., 1998), this effect demonstrated that neural summation effects well matched to behavioral effects can occur at the level of object-specific visual processing as well. While neural summation in visual areas has been reported before (deGelder, 2001; Fort et al., 2002; Minussi et al., 1998; Iacoboni & Zaidel, 2003), these experiments show specific effects at the categorical visual processing level. Behavioral studies have found evidence for beneficial effects of bihemispheric processing of faces (Compton, 2002; Mohr et al., 2002; Schweinberger et al., 2003; Yovel et al., 2003), but the results of Experiment 2 are the first to integrate behavioral effects of faster reactions to redundant compared to mixed category information with activation increased at the respective object-selective areas. The results of Experiment 1 could also rule out alternative explanations as source for the obtained RTE, i.e. stronger bilateral activation patterns based on bihemispheric representation for pictures of faces. Therefore, the results demonstrated that redundancy effects can occur at the specific category level, which are related to an increase in activation of the respective object-selective areas, but are not necessarily based on stronger bilateral activation during bilateral presentation.

Furthermore, the RTE proved to be independent of the exact physical identity of the stimulus. This was true for pictures of faces, as well as pictures of buildings. No significant differences in the reaction times or accuracy were observed for identical pictures versus two pictures from the same category. This independency of exact identity has been reported before (e.g. Marks & Hellige, 2003), but not for this abstraction level of category membership.

Enhanced activation for bilateral redundant presentation was also found in the PPAs for the comparison of two pictures of buildings against word-picture combinations of buildings (Experiment 3). An increase in activation for redundant input from the contralateral visual hemifield is therefore not restricted to redundant versus incongruent category information, but also extends to the same category information in the same versus a different format.

The exact neural mechanism leading to an enhanced activation, however, still needs to be clarified. Firstly, it is possible that enhanced activation is not only based on bilateral input, but also on feedback connections between the left- and right-hemispheric PPAs. Functionally, this would still indicate hemispheric interaction at this level of visual object processing, but could indicate different mechanisms of interhemispheric transfer of information. Recently, it has been suggested, for example, that interhemispheric communication across the CC can be either excitatory or inhibitory between homologous areas of each hemisphere (see Bloom & Hynd, 2005 for a recent review). Since enhanced activation was also observed for the right-lateralized FFA, however, a functional homologue area in the opposite hemisphere does not appear to be necessary for activation increases under bilateral stimulation to occur. For example, it is also possible that the locus of integration of information from both visual hemifields occurs in the superior colliculi

(Corballis, 1998; Savazzi & Marzi, 2004, but see Roser & Corballis 2002).

Secondly, the results from Experiment 1 suggest that different patterns of facilitative and inhibitory influences for unspecific versus incongruent category information modulate FFA and PPA responses. Effects of inhibitory mechanisms have been found in the amplitudes of ERP components. Latencies for bilateral stimulation were faster than for unilateral stimulation, but bilateral stimulation was associated with a smaller amplitude of the ERP components of visual processing than expected by simple linear additivity for LVF and RVF stimulation (Minussi et al., 1998). It is possible, that pictures of faces are of especially high salience (e.g. Lavie et al., 2003) and act therefore as particularly distracting information. Other incongruent category-information (e.g. pictures of animals or tools) presented in the opposite visual hemifield than the pictures of buildings, might result in other patterns of PPA activation. However, since a general increase for bilateral redundant information compared to incongruent information was also found in the PPA for word-picture combinations, the general effect of enhanced activation should be observed for other combinations of incongruent information as well, even though other patterns of relative activation differences are possible under these conditions.

No enhanced activation effects for bilateral stimulation were observed in an area mainly involved in visual word form processing, i.e. the left-lateralized VWFA, in the comparison of picture-word against word-word trials (Experiment 3). As already mentioned, the increase in activation observed in the right-lateralized FFA suggests that lateralization is not an exclusion criterion per se. A possible factor that might account for the absence and presence of an increased activation for bilateral stimulation with written words and

pictures of faces, respectively, is the experimental paradigm used. Bilateral word stimulation was only investigated under semantic matching conditions, whereas bilateral picture presentation for faces was only investigated under a category-detection task. RTEs have been reported for words on lexical decisions tasks, but have mostly been investigated in behavioral tasks (e.g. Hasbrooke & Chiarello, 1998; Mohr et al., 1996; Olk & Hartje, 2001) or neural network modeling (Weems & Reggia, 2004), but not in functional imaging experiments. Hemispheric cooperation mechanisms have been postulated to account for the faster reaction times. If this cooperation is based on bilateral activation during word detection at areas specifically involved in the visual processing of the written words needs to be further investigated with functional imaging measures. The results of Experiment 2, with respect to FFA activation and faster face detection, indicate that an advantage of bilateral stimulation, i.e. interhemispheric cooperation, is not necessarily linked to bilateral activation of homologue areas and the results of Experiment 3 suggest that bilateral word presentation does not automatically lead to bilateral activation of word-specific visual areas.

10.1.2 Modality Specificity of PPA and FFA

Furthermore, it was demonstrated that object-selective areas did not respond in the same category-sensitive way to words naming pictures than to the pictures themselves. This was demonstrated in a passive viewing task, where names of faces and building did not elicit category-specific response in the respective object-selective areas (Reinholz & Pollmann, 2005), and in a more demanding semantic matching task (Experiment 3). While category-specific effects of word presentation were not expected under the rather

shallow processing of the words, enhanced activation was possible under the semantic matching conditions.

Word-picture priming effects have been observed in behavioral tasks (Gordon & Irwin, 2000; Lebreton et al., 2001; Park & Gabrieli, 1995) indicating that some automatic activation of picture-related components can occur, but additional behavioral and functional evidence suggest that this effect is not necessarily based on automatic activation during word reading in the visual object-processing areas. For example, the priming effect seems to depend on the depth of processing. It is stronger or only present for elaborated word processing, i.e. automatic word reading is not sufficient for the priming effect to occur (Hirshman et al., 1990; McDermott & Roediger, 1994; but see Srinivas, 1992). Additionally, functional imaging evidence indicate that the neural side of this priming effect is supposedly located more laterally than the object-selective areas at left temporal regions extending to left frontal regions (e.g. Buckner et al., 2000; Lebreton et al., 2001).

For conditions of 'deeper' semantic processing, in functional imaging studies, comparable activation patterns for words and pictures have been found. For instance, overlapping activation was observed during matching and naming tasks (Bookheimer et al., 1995; Chao et al., 1999; Chee et al., 2000; Perani et al., 1999; Vandenberghe et al., 1996). It has been suggested that activation in object-selective areas can be elicited via top-down modulation (Mechelli et al., 2004), also explaining effects of FFA and PPA activation during visual imagery (Ishai et al., 2002; O'Craven & Kanwisher, 2000). Therefore, it is plausible to assume that top-down processing effects can account for activation of object-selective areas during word reading. While top-down influences are expected to be small during passive viewing of words, they could have been

stronger during semantic matching of pictures and their names. Devlin et al. (2005), for example, found an interaction between category and task for the activation of occipital-temporal areas during word reading. The expected lateral-to-medial activation for words of tools and animals was stronger for the more demanding semantic task than for a less demanding perceptual decision task. The more demanding semantic task in this case, however, was to decide whether the written name was that of a man-made or a natural object. It is unclear, while this category decision obviously lead to greater top-down influences (Mechelli et al., 2004) than the semantic matching task that was used in Experiment 3, where no relative increase for word presentation was observed in the PPAs for the more demanding task. For word-word conditions in Experiment 3, a decision could have been made on perceptual matching, i.e. without an involvement of imagining the actual concept. However, there was no effect of task for the difference in hemodynamic response elicited by picture-picture and picture-word conditions. Thus, even when words had to be matched with pictures, there was no stronger activation difference for picture-only and picture-word conditions in the PPAs for the semantic matching task than for the passive viewing task. The fronto-lateral activation observed under the mixed picture-word conditions could indicate that the information from the VWFA and the PPA was integrated in working memory, i.e. that word and pictures were indeed processed only in the modality specific regions. At this point, however, this explanation is rather speculative. Thus, even though the conditions under which category-specific activation is elicited by visual word processing needs to be established further, the results of these experiments clearly indicate that it is possible to differentiate between activation elicited by pictures and their respective names. This is not only relevant in

supporting the modality-specificity of the areas investigated, i.e. the FFA and PPA, but also encourages the use of pictures and words in the same experimental context, because it was demonstrated that the effects of word reading on activation of object-selective areas are not based on automatic processes, but can instead be controlled experimentally.

10.2 Hemispheric Specialization

Another main finding of the experiments in this dissertation was the effect of a strongly left-lateralized activation for written words presented in the ipsi- as well as contralateral visual hemifield. This hemifield independency replicates findings from Cohen et al. (2000a) and extends these results to different tasks and different stimulus combinations. Along with the left-lateralized activation, the according behavioral effect of a RVF superiority for word presentation was observed. Word-picture matching was more efficient when words were presented in the RVF visual hemifield, i.e. contralateral to the specialized hemisphere, than in the LVF. Both, behavioral and functional imaging data suggested a direct access pattern of interhemispheric processing, i.e. some word processing was carried out in the right hemisphere for words presented contralaterally. Although direct access for word processing has been demonstrated before, this was usually done in behavioral studies (Iacoboni & Zaidel, 1996), or in ERP studies with less precise spatial localization (Schweinberger et al., 1994, but see Katheb et al., 2001). The localization of the right hemispheric activation for words presented in the LVF made it possible to infer that the processing stage was probably comparable to the VWFA because of its almost symmetrical location. This would suggest that words were partly analyzed at a relative high level of visual perception in the right

hemisphere, e.g. at the level of abstract single letter representations (Cohen et al., 2000, 2004; Polk et al., 2002; Puce et al., 1996), but not as efficiently as the visual processing of words in the left-hemispheric VWFA proper. Still, a partial analyses of word-form information could have been sufficient to make a correct response on some trials, leading to the relative faster responses with the hand ipsilateral to word presentation. Since the left-lateralized VWFA was also strongly activated for word-picture conditions, indicated by the significant activation in the baseline contrast, the interaction between left and right hemispheric areas at locations comparable to the VWFA should be investigated further. The results of this experiment show that even though words are usually processed at the left-lateralized VWFA, the right hemisphere is also involved in word processing under specific task conditions. The correspondence between functional imaging and behavioral data with respect to the direct access pattern demonstrates that both approaches can be used to investigate and identify different patterns of interhemispheric interaction.

With respect to hemispheric specialization of object processing, there was evidence for an interaction between task demands and lateralization of FFA activation. While pictures of faces elicited activation bilaterally during passive viewing, in the more demanding face detection task, FFA activation was lateralized to the right hemisphere. Similar evidence for an effect of tasks demands on lateralization of face processing has been obtained in some behavioral studies, where task demands were explicitly manipulated (Moscovitch et al., 1974; Schweinberger et al., 1994), and a behavioral LVF advantage for pictures of faces was only observed under more demanding conditions. However, even though FFA activation was right-lateralized in Experiment 1, there was no

behavioral effect of a LVF superiority for face detection in this experiment. It might be possible, that the behavioral measure were not sensitive enough to detect subtle behavioral differences, for example because of the specific response conditions during fMRI scanning compared to 'purely' behavioral experimental settings. Additionally, the specific stimulation conditions could also have obscured possible visual hemifield effects. While bilateral stimulation could have lead to an increase in existing visual hemifield advantages, this bilateral effect is often observed when the relevant information is spatially cued. In Experiment 2, only the relevant category was cued, but not the relevant visual hemifield. However, even though this could partly account for the absence of a general visual field advantage in the behavioral data, it remains unclear while the right-lateralization of face-specific activation was not associated to visual hemifield advantages of face detection in the left visual hemifield. A general association of FFA responses to detection performance has been reported in other studies (Grill-Spector et al., 2003). Therefore, the FFA activation does not seem to be epiphenomenal to the actual face detection. However, a specific correlation between behavioral and lateralization effects was absent in an ERP study as well (Yovel et al., 2003).

There were no activation peaks in the left inferior temporal cortex or at temporo-polar regions for the simple form of a conjunction analysis for picture-word and word-picture conditions. Activations in these areas have been found in other studies with semantic processing of pictures and words and have been interpreted as site of format-independent semantic processing (Bookheimer et al., 1995; Chee et al., 2000; Moore & Price, 1999; Bright et al., 2004). As discussed in the previous section, it could be the case that the semantic matching task induced a modality specific analysis of the

stimuli and a convergence of information occurred only at higher working memory levels, instead of a modality-independent activation of concepts.

10.3 Hemispheric Control

Another question related to differences in hemispheric interaction patterns was the question of hemispheric control. A specific pattern of hemispheric control could have been observed for bilateral stimulation in the category detection task, because under those conditions both hemispheres had access to the task-relevant information (the detection of only one matching stimulus was sufficient to make a matching decision) and responses could have been dominated by either hemisphere. Hemispheric control, i.e. metacontrol, is often investigated in comparing the response patterns of LVF and RVF trials to response patterns of BIL stimulus presentation, either with respect to an independent variable V (Hellige & Michimata, 1989; Zaidel & Rayman, 1994) or with respect to evidence of specific processing styles of each hemisphere (Hellige et al., 1988; Luh & Levy, 1995). For example, in a matching task with faces, metacontrol was assumed based on an interaction between visual hemifield effects and stimulation conditions, a general LVF advantage for matching chimeric faces was influenced whether the left or right hemisphere was stimulated last, which was interpreted as evidence for differences in hemispheric control (Urgesi et al., 2005). This dissociation between hemispheric competence and hemispheric control has also been reported on other tasks. Error patterns during a consonant-vowel-consonant identification task, for instance, identified right hemispheric control mechanisms, even though the general error rate was lower for direct stimulation of the left hemisphere (Hellige et al., 1989).

In the first experiment, a general RTE was observed, i.e. responses to bilateral stimulation were overall faster than responses to unilateral stimulation. It has been argued that it is impossible to explain bilateral advantages with mechanisms of hemispheric control (Mohr et al., 2002). Furthermore, there were no differences between LVF and RVF stimulation and no interaction with the factor of Condition, i.e. no difference in processing strategy or specific reaction pattern could be observed on unilateral trials which would make an inference from bilateral trials possible. Similar qualitative differences between uni- and bilateral trials have been observed in a series of experiment on rhyming tasks by Banich and Karol (1992), which lead the authors to question the assumption of metacontrol under these conditions.

In the third experiment, behavioral data was only available for the semantic matching task, but not for critical trials during the passive viewing condition. For the semantic matching task, matching two words and two pictures could be qualitatively different (e.g. Snodgrass & McCullough, 1986), so that I would be reluctant to interpret difference in reaction times as indicator of high-level cognitive control conditions. Especially, because matching of two words was theoretical possible based on physical characteristics, even though the stimuli were especially modified to prevent such strategies. However, there was no activation difference in frontomedian areas for word-picture compared to picture-word conditions, i.e. under conditions with less or more efficient direct word processing. A shift from right to left-hemispheric areas of the anterior cingulate cortex could have been a sign of hemispheric control processes, as was demonstrated for verbal and visuo-spatial tasks in another fMRI experiment with a supposedly dominant left and right hemisphere (Stephan et al., 2003). Therefore, the results

of both experiments do not indicate specific hemispheric control processes or a shift in hemispheric control for conditions of direct or indirect stimulation of a specialized hemisphere. However, it cannot be ruled out that hemispheric control mechanisms operated with large variability within subjects or across trials, which has been suggested as explanation for some of the ambiguous findings (Luh & Levy, 1995).

10.4 Final Conclusions and Future Prospects

The response properties of object-selective areas in terms of visual field effects have been rarely investigated in the actual body of research on FFA and PPA activation. The main question of this dissertation was whether there are relative preferences for contra- and ipsilateral stimulation with preferred pictures in the object-selective areas. Moreover, it was asked whether these effects are additionally modulated by the visual information presented in the contralateral visual field. Activation differences between various bilateral stimulation condition were interpreted in the context of different mechanisms and patterns of interhemispheric processing at this level of visual processing.

The work of this dissertation shows that FFA and PPA respond similarly to input from the ipsi- and contralateral visual field, but respond differently to combinations of category-specific and unspecific visual information presented in combination with the preferred stimuli. These results emphasize the importance to consider influences of stimulation from the opposite visual hemifield on activation of object-selective areas, and demonstrate interhemispheric interaction at this processing stage which can result in behavioral advantages of bilateral compared to unilateral processing. Increased activation was observed in both object-

selective areas, i.e. for redundant stimulation with pictures of faces in the FFA and for redundant stimulation with pictures of buildings in the PPA. The increase in activation for bilateral redundant information was observed compared to pairings with incongruent information at the categorical level and, at least for the PPAs, compared to differences in visual format (i.e. picture or word). No increase in activation was obtained for the VWFA. Therefore, an increase in response to bilateral activation could be another feature to determine specificity and functionality of object- or stimulus-specific areas.

Questions for future research should include an investigation of the exact mechanisms responsible for an activation increase during bilateral stimulation. Additionally, the absence of the effect in the VWFA needs to be further investigated. Experiments with bilateral word presentation in a word detection task, and a semantic matching task with pictures of faces would be an interesting continuation of this dissertation. Although redundant target effects have been observed for bilateral presentation of words as well in lexical decision tasks (e.g. Mohr et al., 1996), it could be possible, that a perceptually based RTE under this condition is related to stronger activation at other areas than VWFA processing. Alternatively, the RTE in these tasks could be related to stronger activation at left temporo-polar or frontal areas.

In Experiment 4, a direct access pattern was observed for word-picture combinations, i.e. words were processed at least partly in the right hemisphere. This has been demonstrated before in behavioral tasks (Iacoboni & Zaidel, 1996), and in an additional analysis of electrophysiological data (Schweinberger et al., 1994), but patterns of callosal relay have also been observed (Katheeb et al., 2001). It needs to be determined if there are specific task conditions which

would lead to either direct access or callosal relay for words presented in the LVF.

In two tasks with different demands on the depth of semantic processing, activation of object-selective areas through the written names of the preferred stimulus were unspecific and generally very small. Evidence for activation in object-selective areas during semantic processing of words was found in other studies (e.g. Devlin et al., 2005). The discrepancy between the results need to be clarified, for instance with a parametric manipulation of imageability during word reading.

Overall, the results from these experiments indicate that at the level of object-specific visual processing of pictures, the input from the two visual hemifields can be different than the sum of the unilateral input.

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14 Appendix

Stimuli used in the experiment

	<i>Building</i>	<i>Face</i>
1	Kirche (church)	Kubaner (Cuban)
2	Burg (castle)	Grieche (Greek)
3	Fabrik (factory)	Chinese (Chinese)
4	Hütte (hut)	Franzose (Frenchman)
5	Kiosk (kiosk)	Schotte (Scotsman)
6	Moschee (mosque)	Inder (Indian)
7	Mühle (mill)	Schwedin (Swede)
8	Palast (palace)	Ire (Irishman)
9	Ruine (ruin)	Mongole (Mongol)
10	Schloss (chateau)	Japaner (Japanese)
11	Stadion (stadium)	Spanier (Spaniard)
12	Scheune (barn)	Ägypter (Egyptian)
13	Villa (mansion)	Russe (Russian)
14	Garage (garage)	Däne (Dane)
15	Tempel (temple)	Türke (Turk)
16	Brücke (bridge)	
17	Tunnel (tunnel)	
18	Laube (arbour)	
19	Turm (tower)	
20	Zelt (tent)	

Note: The appropriate English translation is given in parentheses. Stimuli from Number 1 to 15 were used in Experiment 1 and 2; Stimuli from Number 1 to 20 were used in Experiment 3.

Curriculum Vitae

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Selbstständigkeitserklärung

Hiermit erkläre ich, dass die vorliegende Arbeit ohne unzulässige Hilfe und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt wurde und dass die aus fremden Quellen direkt oder indirekt übernommenen Gedanken in der Arbeit als solche kenntlich gemacht worden sind.

Julia Reinholz

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Referat

In einer Reihe von bildgebenden Studien wurde vielfach gezeigt, dass Bilder verschiedener Kategorien spezifische Areale im occipito-temporalen Cortex aktivieren. Spezifische Areale wurden insbesondere für die visuelle Verarbeitung von Bildern von Gesichtern und Bildern von Häusern identifiziert. Für die visuelle Verarbeitung von Wörtern wurde ein potenzielles Wortformareal nahe des linken lateralen occipitalen Sulcus postuliert, in dem Wörter prälexikalisch auf hoher Abstraktionsebene verarbeiten werden.

In der Vielzahl der untersuchten Eigenschaften dieser kategorie- und formatspezifischen Areale wurden mögliche Aktivierungsunterschiede in Bezug auf lateralisierte Darbietung bisher selten thematisiert. Ziel der Dissertation war die Untersuchung objekt- und stimuluspezifischer Areale im Hinblick auf interhemisphärische Interaktion. Dies wurde in insgesamt drei Experimenten mit lateralisierter Darbietung von Bildern und Wörtern der bevorzugten Kategorie und Stimulusformate und der Methode der funktionellen Magnetresonanztomographie untersucht.

In drei fMRT-Experimenten konnte die spezifische Aktivierung verschiedener Areale für die visuelle Verarbeitung von Bildern von Gesichtern, Gebäuden und Wörtern repliziert werden. Unter verschiedenen Aufgabenanforderungen und Bedingungen wurde untersucht, inwieweit sich die lateralisierte Darbietung von Bildern der

bevorzugten Kategorie auf Aktivierungen der jeweils relevanten objekt-spezifischen visuellen Areale auswirkte. Außerdem wurde für die Darbietung von Wörtern untersucht, ob sich Aktivierungsunterschiede für kontra- und ipsilaterale Präsentation auf ein stark links-lateralisiertes potentiell Wortformareal auswirkte und welche Formen interhemisphärischer Interaktion sich im Zusammenhang mit dieser linkshemisphärischen Spezialisierung ergab. Für die Verarbeitung von Wörtern wurde ebenfalls untersucht, ob sich beim Lesen der Bildbezeichnungen unter unterschiedlichen Verarbeitungsanforderungen kategoriespezifische Aktivierungen in den entsprechenden objekt-verarbeitenden Arealen zeigen lässt, die zum Beispiel auf Grund von visueller Vorstellung top-down moduliert ist.

Insgesamt konnte gezeigt werden, dass sich die Präsentation unterschiedlicher Information im gegenüberliegenden visuellen Halbfeld auf die Aktivierung der entsprechenden objekt-verarbeitenden Areale für Bilder bevorzugter Kategorien auswirkte. Dabei ergab sich über verschiedene Aufgaben und Stimulationsbedingungen hinweg der Effekt einer erhöhten Aktivierung für bilateral redundante Präsentation im Vergleich zur Präsentation inkongruenter Kategorieninformation, sowohl für die PPAs als auch die FFA.

Für ein Areal, das spezifisch an der visuellen Verarbeitung geschriebener Wörter beteiligt ist, ergaben sich keine Effekte einer gesteigerten Aktivierung für die bilaterale Wortstimulation. Die Evidenz eines solchen Effektes für die FFA spricht aber dagegen, dass homologe Aktivierung in der anderen Hemisphäre eine Voraussetzung für das Auftreten dieser erhöhten Aktivierung sind.

In einer semantischen Vergleichsaufgabe ergab sich ein Zusammenhang zwischen lateralisierter spezifischer visueller

Verarbeitung und Verhaltenseffekten einer schnelleren Reaktion bei Wortpräsentation im linken visuellen Halbfeld. Der direkte Kontrast beider Bedingungen, sowie spezifischer Verhaltenseffekte ergab Evidenz für interhemisphärische Interaktion im Sinne eines direct access Modells.

Die Unterschiede in den Aktivierungsmustern für die PPA und FFA für unterschiedliche Kombinationen bilateraler Stimulation zeigen, dass die Aktivierungen in den objekt-spezifischen Arealen beeinflusst werden von Informationen aus beiden visuellen Halbfeldern. Die beobachteten Aktivierungsunterschiede stimmten dabei gut mit den gleichzeitig erhobenen Verhaltensdaten hinsichtlich eines Reaktionszeitvorteils, als auch hinsichtlich des Musters von hemisphärischer Spezialisierung und interhemisphärischer Verarbeitung lateralisierte Informationen im Sinne eines direct access.

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