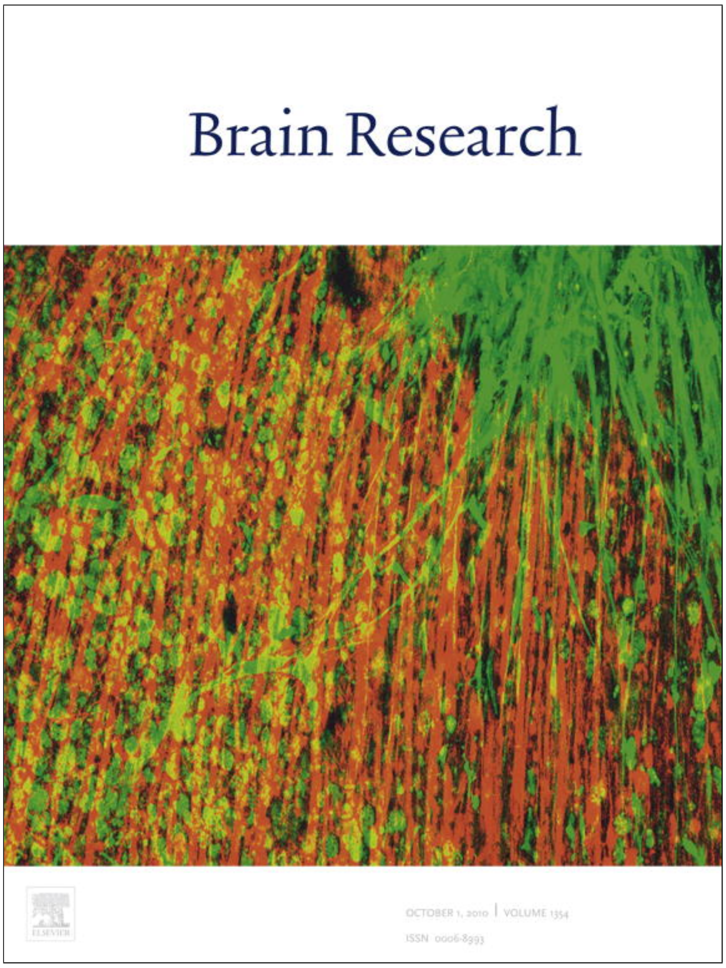
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Research Report

Differences in cerebral activation during perception of optokinetic computer stimuli and video clips of living animals: An fMRI study

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ABSTRACT

Aims: There is behavioral evidence of increased spontaneous recruitment of visual attention to ancestral evolved categories, such as animals, compared with expertise-derived categories, such as a computer. In order to investigate the association between visual perception and spontaneous visual attention, a study was performed to determine if brain activation whilst viewing moving animals was increased compared with optokinetic computer stimuli. *Methods*: Functional MRI was performed in 12 healthy volunteers using a standard block-design paradigm, consisting of three consecutive experiments. Subjects viewed the following images: Experiment one — optokinetic computer stimuli alternating with static computer stimuli; Experiment two — moving animals alternating with non-moving animals; Experiment three — moving animals alternating with optokinetic computer stimuli. *Results*: Moving animals evoked motion-dependent activation bilaterally in the middle and superior temporal gyri, right inferior temporal gyrus, left occipital gyrus, right supramarginal gyrus, and left straight gyrus. Integrated object-and-motion-dependent activation was found bilateral in inferior and middle temporal gyri, right superior temporal gyrus, right superior parietal lobule, left dorsal putamen, and right amygdala. *Conclusions*: These results suggest that there is increased cerebral activity in the visuo-attentional network whilst viewing moving animals compared with optokinetic computer stimuli.

1. Introduction

There has been comparatively little research into whether there is an increase in spontaneous recruitment of visual attention to animate categories (i.e. human and non-human animals) compared with inanimate categories (i.e. tools), and whether such recruitment might be based on evolved prioritization (New et al., 2007; Rees, 2008). Ancestrally derived

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selection criteria develop during evolution to ensure survival and reproduction of a species. With regard to the animate monitoring hypothesis, this should cause stronger spontaneous recruitment of attention to animals than to inanimate objects, regardless of their current utility. Empirically derived criteria develop during ontogeny to enhance task performance. According to the expertise hypothesis, this should cause stronger spontaneous recruitment of attention to task-relevant objects of current utility than to task-irrelevant stimuli, regardless of their liveliness. In the behavioral study of New et al. (2007) healthy subjects detected changes in animals substantially quicker and more reliably than changes in inanimate objects, such as vehicles, buildings, or tools. This animate monitoring bias could not be accounted for by differences in lower level visual characteristics or expertise. These findings provide important insights into the functional organization of the human visual system; however, the precise neuronal basis of the monitoring processes is not yet known. Neuroimaging studies on the processing of visual stimuli, which consisted of animals, revealed a wide distribution of neural networks, including the frontal, temporal, parietal, and occipital regions (Humphreys and Forde, 2001; Devlin et al., 2002; Chan et al., 2004).

The computer is an evolutionarily novel contrast category with which subjects now have a great deal of experience. Computer stimuli frequently consist of abstract signs (i.e. letters and graphical signs), in some software programs with moving elements (i.e. training tools for visual perception and attention). A recent functional MRI (fMRI) study investigated the neuronal basis of visual motion processing in healthy volunteers during optokinetic stimulation, using a vertical stripe pattern generated by a computer program (Kikuchi et al., 2009). Increased cortical activation was observed in the primary visual cortex and visual association areas, superior parietal lobule and frontal eye fields.

The aim of the present pilot fMRI study was to investigate brain activation patterns during observation of ancestral stimuli (videos of real animals) compared with modern stimuli (optokinetic patterns on a computer monitor), in healthy volunteers. It was hypothesized that cerebral activation would be increased when viewing images of moving animals compared with cerebral activation whilst viewing optokinetic computer stimuli.

2. Results

The first experiment explored motion-dependent activation whilst subjects viewed optokinetic computer stimuli compared with static computer stimuli. Superior activation was observed in the left striate area 17, right inferior occipital gyrus (BA 19), right and left inferior temporal gyrus (BA 37), right middle temporal gyrus (BA 37), right and left parietooccipital transition zone (BA 19/39), and right superior parietal lobule (BA 7), when analyzed using the one-sample t-test (corrected P-value <0.05). Table 1 provides a summary of the activated areas, including Talairach coordinates and z-values.

The second experiment investigated motion-dependent activation during observation of moving animals compared with non-moving animal stimuli. Superior activation was seen in the right and left inferior and middle occipital gyrus (BA 18), right and left fusiform gyrus, right and left parietooccipital transition zone (BA 19/39), right and left superior parietal lobule (BA 7), right middle frontal gyrus (BA 6), right inferior frontal gyrus (BA 9), and right medial orbital gyrus (BA 11), according to the one-sample t-test (corrected P-value <0.05) [Table 1].

Table 1 – Activated areas whilst observing moving stimuli compared with static stimuli in the computer and animal tasks, analyzed using the one-sample t-test.

Condition	Gray matter	Side	BA	Talairach coordinates (mm)	z-Value
Computer: moving stimuli versus static stimuli; one-sample t-test ($P<0.05$ corrected)	Striate area	L	17	−8; −90; −12	4.96
	Occipital	R	19	26; −78; −12	6.36
	Inferior temporal	R	37	50; −68; −2	5.81
	Inferior temporal	L	37	−44; −70; −6	5.37
	Middle temporal	R	37	50; −64; 20	5.73
	Parietooccipital transition zone	R	19/39	26; −76; 38	4.56
	Parietooccipital transition zone	L	19/39	−26; −84; 38	4.83
	Parietooccipital transition zone	L	19/39	−38; −80; 18	7.70
	Superior parietal lobule	R	7	16; −66; 60	6.03
Animal: moving stimuli versus static stimuli; one-sample t-test ($P<0.05$ corrected)	Occipital	R	18	28; −92; 8	15.68
	Occipital	R	18	22; −88; −12	14.87
	Occipital	L	18	−32; −92; 10	7.16
	Occipital	L	18	−20; −90; −8	6.85
	Fusiform	R		50; −52; −18	9.18
	Fusiform	L		−42; −50; −20	8.14
	Parietooccipital transition zone	R	19/39	26; −82; 42	10.29
	Parietooccipital transition zone	L	19/39	−18;−80; 42	9.51
	Superior parietal lobule	R	7	24; −52; 68	5.21
	Superior parietal lobule	L	7	−16; −60; 70	5.30
	Middle frontal	R	6	38; 0; 56	8.56
	Inferior frontal	R	9	46; 10; 22	7.78
	Medial orbital	R	11	22; 36; −18	5.24

R = right, L = left, BA = Brodmann area, and z-values of local activity peaks.

The third experiment explored motion-dependent activation comparing moving animals with optokinetic computer stimuli directly. Superior activation was observed in the left inferior occipital gyrus (BA 19) (Fig. 1A, coronal view), right inferior temporal gyrus (BA 37) (Fig. 1A, transversal view), right and left middle temporal gyrus (BA 37), and right and left superior temporal gyrus (BA 22) (Fig. 1A, 1st sagittal view), when analyzed using the one-sample t-test (uncorrected P-value<0.001). Additionally, superior activation was observed in the right parietal operculum (supramarginal gyrus; BA 40) and left straight gyrus (BA 11) (Fig. 1A, 2nd sagittal view). Table 2A provides a summary of the activated areas, including Talairach coordinates and z-values. There were no significant activations when the optokinetic computer stimuli, as the active condition, were compared with moving animals, as the control condition.

Object-and-motion-dependent activation was investigated by comparing the results from the first and second experiments using a paired t-test with an uncorrected P-value<0.001. The analysis revealed condition-specific differences in two comparisons. In the first comparison optokinetic computer stimuli as the active condition were compared with moving animal stimuli, as the control condition, using a paired t-test and uncorrected P-value<0.001. Superior activation was found only in the frontal operculum and insula in the right and left hemispheres (BA 44) (Table 2B; Fig. 1B). In the second comparison contrasting moving animal stimuli as the active condition with optokinetic computer stimuli as the control condition, superior activation was observed within a posterior section of the right hemisphere in the middle temporal gyrus (BA 37), extending to the inferior temporal gyrus (BA 37), fusiform gyrus, middle occipitotemporal junction (BAs 19, 37; area MT), and occipital gyri (BAs 18, 19) (Fig. 1C, transversal view). In a more anterior section significant activation was seen in the right superior temporal gyrus (BA 22) (Fig. 1C, sagittal view), and the right inferior temporal gyrus (BA 20). In an anterior section of the right hemisphere there was significant activation in the middle temporal gyrus (BA 21), extending to the inferior temporal gyrus (BA 20) at the end of the ventral path. Further superior activation for moving animal stimuli compared with optokinetic computer stimuli was found within a posterior section of the left hemisphere in the middle temporal gyrus (BA 37), extending to the inferior temporal gyrus (BA 37), and the occipital gyri (BAs 18, 19). In a more anterior section superior activation was found in the left inferior temporal gyrus (BAs 20, 21), extending to the left fusiform gyrus. Additionally, superior activation was found in the right superior parietal lobule (BA 7), left dorsal putamen, and right amygdala (BA 28) (Fig. 1C, coronal view), for moving animal stimuli compared with optokinetic computer stimuli. A summary of animal-specific activated areas, which overall were more extensive in the right hemisphere than in the left hemisphere, including the Talairach coordinates and z-values is provided in Table 2C.

3. Discussion

This study in 12 healthy volunteers investigated the neuronal processes underlying visual perception of ancestral and expertise-derived stimuli, by evaluating differences in brain

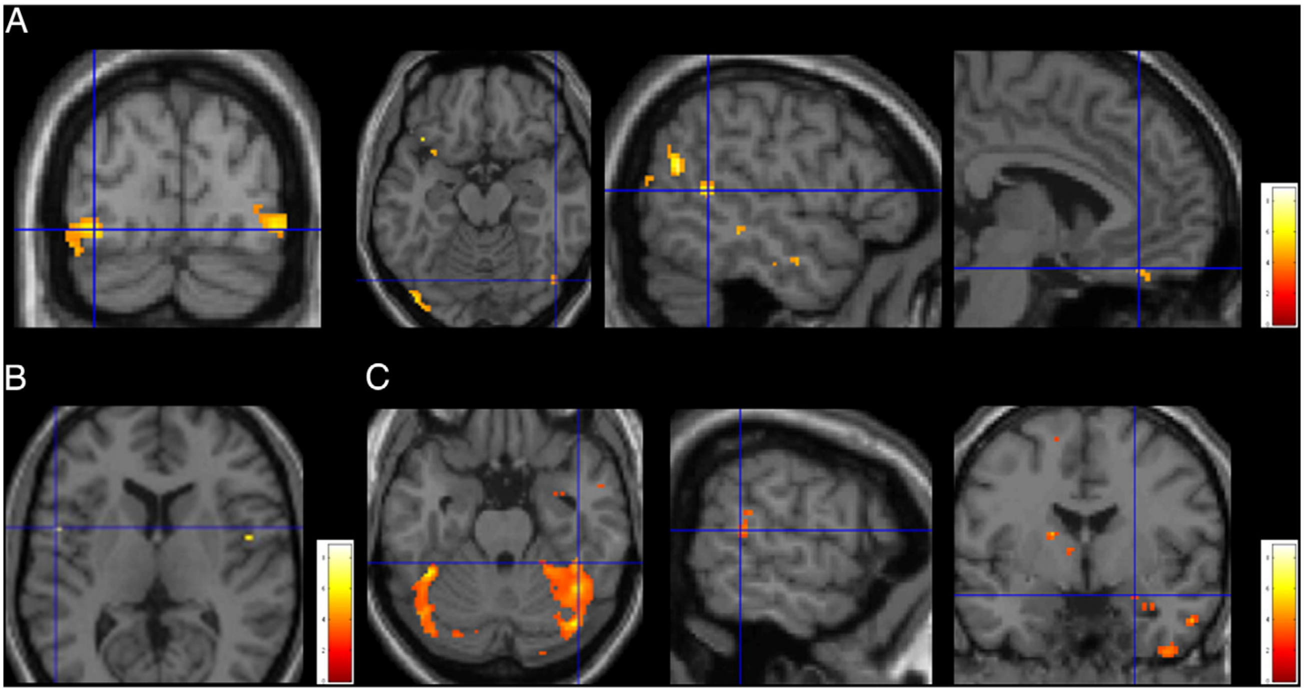

Fig. 1 – Increased activity in healthy volunteers during viewing. A. Moving animals directly compared to optokinetic computer stimuli (motion-dependent effect), B. optokinetic computer stimuli compared to moving animal stimuli (object-and-motion-dependent effect), and C. moving animals compared to optokinetic computer stimuli (object-and-motion-dependent effect). The activated areas are superimposed on a standard T1 weighted image. P-value was 0.001 uncorrected.

Table 2 – Activated areas whilst comparing moving stimuli in the animal and computer tasks, analyzed by the one-sample t-test and paired t-test.

Condition	Gray matter	Side	BA	Talairach coordinates (mm)	z-Value
A. Animal stimuli versus computer stimuli: one-sample t-test (P<0.001 uncorrected)	Occipital	L	19	−32; −86; −8	6.11
	Inferior temporal	R	37	50; −78; −4	7.03
	Inferior temporal	R	37	48; −70; −16	4.36
	Middle temporal	R	37	50; −78; 12	7.03
	Middle temporal	L	37	−38; −70; 16	7.31
	Superior temporal	R	22	52; −36; 16	8.53
	Superior temporal	L	22	−52; −60; 22	7.23
	Superior temporal	L	22	−52; −46; 10	6.19
	Parietal operculum	R	40	50; −36; 30	7.01
	Straight gyrus	L	11	−4; 38; −20	4.99
B. Computer stimuli versus animal stimuli: paired t-test (P<0.001 uncorrected)	Frontal operculum, insula	R	44	48; 0; 6	3.36
	Frontal operculum, insula	L	44	−52; 6; 8	3.92
C. Animal stimuli versus computer stimuli: paired t-test (P<0.001 uncorrected)	Inferior temporal	R	20	42; −40; −24	6.60
	Inferior temporal	L	20/21	−40; −46; −24	8.25
	Middle temporal	R	37	46; −66; 2	7.33
	Middle temporal	R	21	52; 0; −32	6.62
	Middle temporal	L	37	−48; −72; 6	7.77
	Superior temporal	R	22	64; −40; 12	5.37
	Superior parietal lobule	R	7	28; −48; 52	6.84
	Dorsal putamen	L		−20; −4; 10	5.15
	Amygdala	R	28	26; −2; −18	4.25

R = right, L = left, BA = Bordmann area, and z-values of local activity peaks.

activation during observation of moving animal stimuli compared with optokinetic computer stimuli. The main results showed that perception of moving animals as compared with optokinetic computer stimuli increased activation of the visual neural network bilaterally. Thereby, specific effects of biological motion were found in superior and middle temporal regions, and integrated effects of object and motion in the inferior occipitotemporal pathway. These activations in the visual system were combined with increased activations in the right somato-sensory region, as well as in structures related to visual attention, incentive motivation, reward experiencing and positive emotion (right posterior parietal cortex, left putamen and right amygdala). The results are thought to be valid, because the sample size of 12 subjects exceeds that recommended in fMRI studies; individual variations are within the statistical model, and spatial solution is highly sensitive (compare Sections 4.3 Image acquisition and 4.4 Image analysis; Friston et al., 1999a).

In neuropsychological lesion studies, which investigated the processing of living visual stimuli (animals) compared with inanimate visual stimuli (e.g. tools), lower level visual characteristics were taken into account, i.e. luminance, color, number of details, semantic complexity and frequency of the stimuli (Farah et al., 1991; Laiacona et al., 1993; Caramazzo and Shelton, 1998). With the exception of color in the present fMRI study these factors could not be accounted for due to the inherent differences between the ancestral animal stimuli and modern computer stimuli. However, the present study did not investigate the specific neuronal mechanisms for processing these lower level visual characteristics. Rather, the main objective was to compare motion-dependent as well as object-and-motion-dependent effects on neuronal activation patterns during the visual perception of the ancestral and expertise-derived stimuli as a whole. In the behavioral study of New et al. (2007), increased spontaneous recruitment of visual attention to animals compared with inanimate objects was observed. As far as we know, there is no other fMRI study comparing optokinetic stimulation with video presentation of living animals. The results will be discussed with regard to the functional relevance of the main activated areas, comparing the moving scenes between the animal and computer.

Regarding the specific motion-dependent effect observed in the direct comparison of animal biological movements in a three-dimensional space and computer dots moving along a horizontal axis, the main focus of activation was bilaterally in the superior and middle temporal gyri (BAs 22, 37) (Table 2A; Fig. 1A, 1st sagittal view). Significant activity in the middle temporal gyrus (area MT) has also been seen in a PET study of novel objects moving in a three-dimensional space compared with objects moving along a horizontal axis (Cornette et al., 1998). Specifically, significant activation in the superior temporal gyrus/sulcus and parts of the middle temporal gyrus (BAs 22, 37) has been shown to be associated with the vision of biological motion in fMRI studies, presenting point-light displays of moving persons compared with scrambled versions of the same animations (Jokisch et al., 2005; Saygin, 2007). An additional significant activation found in these studies, as well as in the present study, was observed in the right parietal operculum (supramarginal gyrus; BA 40). The inferior parietal cortex, particularly in the right hemisphere, has been shown to be associated with spatial attention in fMRI studies in healthy subjects directing attention to right- and left-sided locations (Gitelman et al., 1999; Perry and Zeki, 2000; Malhotra et al., 2009). In terms of integrating spatial attention with motivational information, the spatial attention network (particularly the posterior parietal cortex) has been shown to interact with the limbic system (especially the orbitofrontal cortex) (Mohanty et al., 2008). Accordingly, in the present study there was increased activation in the left straight gyrus (BA 11) during observation of the moving animal stimuli (Fig. 1A, 2nd sagittal view). Medial orbitofrontal cortex (straight gyrus) activity had been shown to be related to the monitoring of subjective pleasantness and affective value of different reinforcers, in a meta-analysis of neuroimaging studies (Kringelbach and Rolls, 2004).

With regard to the integrated object-and-motion-dependent effect, when the optokinetic computer stimuli were compared with the moving animals, selective activation was only observed in the frontal operculum and insula in both hemispheres (BA 44) (Table 2B; Fig. 1B). These regions have been shown to be associated with explicit effort, central command and control for action (Williamson et al., 2003). In the present study, more executive control functions may be required during observation of the computer stimuli than the animals. Moreover, the prefrontal cortex and the right fronto-insular cortex, in particular, play a critical role in the ability to switch attentional control across changing stimulus modalities, as across the present animal and computer stimuli (Rossi et al., 2009; Sridharan et al., 2008).

Conversely, when the moving animals were compared with the optokinetic computer stimuli, the main focus of activation was more intensive in the right than in the left hemisphere, within the ventral visual system from posterior to anterior in the occipital gyri, the middle occipitotemporal junction, the middle and inferior temporal gyri, and the fusiform gyrus (BAs 18, 19, 37, 20, 21) (Table 2C; Fig. 1C, transversal view). Activation in the infero-lateral and anterior–medial cortices has been related to the perception and cognitive processing of visual stimuli, which consisted of animals in other neuroimaging studies (Chan et al., 2004). Generally, experience with a dynamic environment has caused adjustment of the human visual system to use form and motion as complementary sources of information for moving object recognition. A recent study of the integration of higher order form and motion by the human brain revealed a visual processing hierarchy, with the lateral occipitotemporal cortex representing an object's three-dimensional structure, and the anterior fusiform and posterior middle temporal regions being involved in spatio-temporal integration of form and motion during dynamic object processing (Sarkheil et al., 2008). In the present study the animals were presented as real moving objects, not as point-light displays as in the studies of structure-from-motion-perception by Jokisch et al. (2005) and Saygin (2007). This may explain the differences in activated regions in the direct comparison of moving animals and optokinetic computer stimuli revealed by the one-sample t-test in the third experiment (Fig. 1A, 1st sagittal view), and the comparison between the moving animals and optokinetic computer stimuli revealed by the paired t-test for the first and second experiments (Fig. 1C, transversal view). The first comparison showed specific motion-dependent activation in the superior and middle temporal regions; the second comparison revealed the integration of object-and-motion-dependent activity in occipital, inferior and middle temporal, as well as fusiform regions.

Regarding the integrated object-and-motion-dependent effect comparing the moving animals and optokinetic computer stimuli, further significant activation was only observed in the right, but not in the left, hemisphere in the superior temporal sulcus and superior temporal gyrus (BA 22) (Fig. 1C, sagittal view). The right hemisphere has been thought to subserve specific analysis of biological motion patterns, which provides information of social and emotional relevance (Jokisch et al., 2005; Saygin, 2007). One explanation might be that the superior temporal sulcus is reciprocally connected with the amygdala (Sato et al., 2004). The emotional aspect may also play a role in the present animal condition.

Furthermore, when the moving animal stimuli were compared to the optokinetic computer stimuli there was significant activation in the left dorsal putamen (Fig. 1C, coronal view). Activation in the dorsal striatum has been reported in response to pleasant pictures, initiation of spontaneous movements, enjoyable activities, and reward experiencing (Rolls, 2000). An explanation might be that the putamen receives rich efferent projections from mesolimbic dopaminergic neurons (Schmidt et al., 2008). This mechanism is more crucial for incentive motivation than for executive control; incentive motivation is supposed to be of substantial relevance in the studied animal condition.

When the moving animal stimuli were compared with the optokinetic computer stimuli there was also significant activation in the right amygdala (Fig. 1C, coronal view). Besides the occipital cortex and the fusiform gyrus, the amygdala has been shown to be associated with emotions induced by visual stimuli, e.g., dynamic facial expressions (Phan et al., 2002; Winston et al., 2003). This associative connection between the occipital lobe and the anterior temporal lobe appears to mediate the fast transfer of visual signals to anterior temporal regions, and neuro-modulatory back-projections from the amygdala to early visual areas (Catani et al., 2003). Additionally, amygdala activity has been shown to be affected by the level of attentional processing, as passive processing was associated with a higher probability of amygdala activation than active task instructions (Costafreda et al., 2008). Thus, in the present study subjects were instructed to observe the stimuli in a relaxed manner.

In line with the increased spontaneous recruitment of visual attention to moving animals compared to inanimate objects observed on the behavioral level (New et al., 2007), the present fMRI study shows motion- and object-dependent effects on increased neuronal activity during processing of visual stimuli, consisting of moving animals compared with optokinetic computer stimulation. It may be hypothesized that these results could be of relevance with regard to the current utility of optokinetic stimulation for visual perception training in the neurorehabilitation of neglect patients. These patients frequently suffer from anosognosia and auto-activation deficit. Loss of explicit effort and self-driven behavior may be reversed by increasing the spontaneous recruitment of visual attention. Single-case studies of patients with severe left-sided neglect after a stroke in the right middle cerebral artery territory, showed that domestic animals had an increased effect on the perception of the neglected hemispace compared to optokinetic computer stimuli with simple shapes and a moving random dot pattern (Böttger, 2008). In this context a recent therapy outcome study is also of interest, which investigated visual restoration through extrastriate stimulation in patients with visual field defects (Jobke et al., 2009). It was shown that stimulus detection improved with massive stimulation of the entire region of blindness by a moving spiral compared with single-point visual stimulation, which was restricted to areas of residual vision. As in the present study, the authors used stimulation patterns which differ with respect to size of the visual objects, their distribution in the visual field and movement. The greater improvement of visual perception after the massive spiral-like stimulation was interpreted as an activation of extrastriate pathways. However, as in the neglect study (Böttger, 2008), there are no neuroimaging data for evaluating the cerebral activation patterns in these patients.

One limitation of the present study is that there are no fMRI data showing whether stimulation with visual patterns, consisting of domestic animals, results in comparable activations in neurological patients as in healthy volunteers. Therefore, further fMRI studies are needed to investigate whether the neuronal activation pattern observed in healthy volunteers might be replicated in stroke patients with neglect and auto-activation deficit, and if so, whether these activation patterns might correlate with improvements of perception behavior when treated. Such combinations of basic and clinical science data are highly relevant to the field of stroke rehabilitation (Hummel and Cohen, 2005). Another limitation of the present experimental design is that the differences in cerebral activation, revealed by optokinetic computer stimulation and the moving animal stimuli cannot be interpreted meaningfully with regard to emotionality. In the present study there was increased cerebral activation in emotionally relevant structures such as the amygdala, putamen and gyrus rectus. In order to control the neuronal processes underlying emotionality whilst viewing animals in an fMRI experiment, it is necessary to use comparable stimulation patterns with the presence and absence of emotional cues such as eyes and faces. This could be done using stimulus material consisting of clips of real animals compared to point-light displays of moving animals, similar to the point-light displays of moving persons in the studies of Jokisch et al. (2005) and Saygin (2007), and would require an additional fMRI study.

4. Experimental procedures

4.1. *Subjects*

Three male (mean age 42 years, range 42–43) and 9 female healthy volunteers (mean age 33 years, range 23–47) were studied. Questioning revealed that 9 subjects were right-handed, 1 was left-handed and 2 were ambidextrous. Five subjects had high level of education and 7 a middle level. Seven subjects lived alone and 5 in partnership. There was no evidence of brain tissue abnormality on structural MRI, and none of the subjects had a history of neurologic or psychiatric disease. The attitude towards animals was positive in 8 subjects and neutral in 4 subjects. Seven subjects owned or had owned one or more domestic animals. The attitude towards a computer was positive in 4 subjects and neutral in 8 subjects. Ten subjects used the computer every day, and 2 subjects every week. Informed written consent was obtained prior to scanning. The study was conducted in accordance with the Declaration of Helsinki.

4.2. *Experimental design*

During stimulation subjects were asked to lie relaxed inside the scanner and to view the presented stimuli in the absence of instructions. The stimulus material consisted of colored photos and colored silent video sequences. The animal tests included photos and videos of domestic animals (dogs and rabbits) moving on a platform in front of a uniform bright background. The computer tests included photos and videos of stimuli in front of a uniform bright background presented on the PC monitor. The stimuli consisted of one or more targets (forms, symbols and objects) with a random dot pattern flowing to the left or right side coherently (OK neglect training; www.psycware.info/therneuropsy/therneuropsy.html). This special software is used for visual exploration training in standard neglect rehabilitation (Kerkhoff et al., 2006). Furthermore, the task was chosen because, similar to biological motion processing, it is thought to tap into extrastriate neural correlates (Braddick et al., 2001), and to involve temporal and spatial integration of motion elements. Though there is perceived coherence defined by the moving dots, these stimuli do not define an object or animal.

The experiment was based on a block design consisting of three consecutive experiments. Each experiment was divided into eight epochs (on–off periods) starting with the control condition. Active periods were alternated with control periods every 31 s; each active period lasted 31 s. Experiment 1 used optokinetic computer stimuli as the active epoch alternating with static computer stimuli in the passive epoch. Experiment 2 used moving animals as the active epoch alternating with animal photos in the passive epoch. Experiment 3 was optokinetic computer stimuli as one epoch alternating with moving animals in the other epoch. The order of experiments was randomized.

Before beginning the scanning each subject answered a questionnaire about attitudes towards animals and computers (positive, neutral, and negative), ownership of domestic animals and frequency of using a computer.

4.3. *Image acquisition*

All MR images were acquired using a 1.5-Tesla scanner (Sonata, Siemens, Erlangen, Germany). Stimuli were presented using a scene viewed inside the scanner room and beamer projection from outside. A mirror was fixed on the headcoil. A 3D FLASH sequence (TR 10 ms, TE 4.5 ms, flip angle 30°, FOV 240 mm, matrix 512, slice-thickness 1.5 mm) was acquired for individual co-registration of functional and structural images. BOLD contrast images were acquired using an echo-planar technique (TR 3100 ms, TE 50 ms, flip angle 90°, FOV 240 mm, matrix 64), with 34 transversal slices angulated in the direction of the corpus callosum with a thickness of 3 mm and a 0.3 mm slice gap. Three “dummy” scans were eliminated prior to data analysis to account for T1 relaxation effects.

4.4. *Image analysis*

Before entering the images in the statistical parametric map (SPM) software they were inspected for disturbances due to magnetic susceptibility in frontal and basal regions. For data analysis, SPM 02 software (Wellcome Department of Cognitive Neurology, London, UK) was used. Prior to statistical analysis, images were realigned using sinc interpolation and normalized to the standard stereotactic space, corresponding to the template from the Montreal Neurological Institute (http://www.mrc-cbu.cam.ac.uk/Imaging/mnispace.html). Bilinear interpolation was applied for normalization. The images were smoothed with an isotropic Gaussian kernel of 9 mm. Statistical modeling and interference were based on the general linear model approach (Friston et al., 1995a). Conditions were modeled as epochs, using a boxcar regressor convolved with the hemodynamic response function (hrf), and the corresponding temporal derivative. High-pass filtering with a cut-off frequency of 120 s and low-pass filtering with the hrf was applied.

Single subject analyses provided contrast images on the task-related effects for each perception condition. Significant signal changes for each contrast were assessed by means of t-statistics on a voxel-by-voxel basis and maximum likelihood estimation, as commonly used for fMRI (Friston et al., 1995b; Friston et al., 1999b). The resulting set of voxel values for each contrast constituted an SPM of the t-statistic. Following single subjects analyses, second level random effects were calculated with the single subject contrast images (Friston et al., 1999a). The resulting contrast images of individual contrasts revealed by the voxel-by-voxel analysis were entered into a one-sample t-test for comparison of the active and control conditions in the first two experiment designs ($p<0.05$ corrected), exploring motion-dependent activation both in the computer and the animal tasks. The resulting contrast images of individual contrasts were entered into a one-sample t-test for direct comparison of the active and control conditions in the third experiment ($p<0.001$ uncorrected), exploring motion-dependent activation contrasting the animal and computer tasks. Doing this, regions of interest (ROIs) were the activated areas in the one-sample t-tests for comparison of the active and control conditions in the first two experiments, selectively. The resulting contrast images of individual contrasts were also entered into a paired t-test for comparison of the active and control conditions in the first two experiment designs. Two contrasts were computed to explore object-and-motion-dependent activation. Perception of optokinetic computer stimuli was contrasted with perception of moving animals and vice versa. The null hypothesis was that perception of animals and computer stimuli had identical group means. The threshold of the t-statistic was set to $p<0.001$ uncorrected for multiple comparisons for a priori ROIs.

The ROIs were widely localized and included the temporal, parietal and insular cortices. For visual perception, visual attention and visually induced emotion, the activations of the following brain regions have been reported in humans: occipital gyri, fusiform gyrus, inferior and superior temporal cortex, and parietal lobules, particularly in the right hemisphere, (Lang et al., 1998; Bradley et al., 2003; Lane et al., 1999; Kastner and Ungerleider, 2000; Saygin, 2007) as well as limbic regions (Phan et al., 2002). Resulting T-maps were superimposed upon a high resolution anatomical T1 mean image included in SPM 02. Coordinates of significant voxels were transformed to Talairach space (Talairach and Tournoux, 1988) and verified by visual control. Local maxima were assigned to anatomical structures and Brodmann areas (BAs) using the Talairach Daemon software (Lancaster et al., 1997).

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