

Cognition and Neurosciences

An fMRI study of working memory for schematic facial expressions

HARALD BENEVENTI,¹ ROGER BARNDON,³ LARS ERSLAND^{4,5} and KENNETH HUGDAHL^{1,2}¹Department of Biological and Medical Psychology, University of Bergen, Norway²Division of Psychiatry, Haukeland University Hospital, Bergen, Norway³Department of Radiology, Haukeland University Hospital, Bergen, Norway⁴Department of Clinical Engineering, Haukeland University Hospital, Norway⁵Department of Surgical Sciences, University of Bergen, Bergen, Norway

Beneventi, H., Barndon, R., Ersland, L. & Hugdahl, K. (2007). An fMRI study of working memory for schematic facial expressions. *Scandinavian Journal of Psychology*, 48, 81–86.

Functional magnetic resonance imaging (fMRI) was used to examine neuronal activation in relation to increasing working memory load in an n-back task, using schematic drawings of facial expressions and scrambled drawings of the same facial features as stimuli. The main objective was to investigate whether working memory for drawings of facial features would yield specific activations compared to memory for scrambled drawings based on the same visual features as those making up the face drawings. fMRI-BOLD responses were acquired with a 1.5 T Siemens MR scanner while subjects watched the facial drawings alternated with the scrambled drawings, in a block-design. Subjects had to hold either 1 or 2 items in working memory. We found that the main effect of increasing memory load from one to two items yielded significant activations in a bilaterally distributed cortical network consisting of regions in the occipitotemporal cortex, the inferior parietal lobule, the dorsolateral prefrontal cortex, supplementary motor area and the cerebellum. In addition, we found a memory load \times drawings interaction in the right inferior frontal gyrus in favor of the facial drawings. These findings show that working memory is specific for facial features which interact with a general cognitive load component to produce significant activations in prefrontal regions of the brain.

Key words: Emotions, fMRI, face processing, working memory.

Kenneth Hugdahl, Department of Biological and Medical Psychology, University of Bergen, Jonas Lies vei 91, N-5009 Bergen, Norway. Fax: +47-55589872; e-mail: hugdahl@psybp.uib.no

INTRODUCTION

Working memory (WM) has been proposed to be a limited capacity system which temporarily maintains and manipulates verbal and visuospatial information on-line. It is supposed to support human thought processes by providing an interface between perception, long-term memory and ultimately action. Action is in addition influenced by emotion and according to Baddeley (2003) emotional control of working memory is also crucial, but a largely ignored subject.

Information processing in working memory is supposed to be carried out by different unique subcomponents. Maintenance is accomplished by two basic subsystems – *the phonological loop* and *the visuospatial sketch pad*, for remembering verbal and visuospatial information, respectively. These subsystems are further subdivided into passive storage and active rehearsal processes. Behavioral and neuropsychological evidence have also suggested a dissociation between spatial and visual information (Darling, Della Sala, Logie & Cantagallo, 2006; Della Sala, Gray, Baddeley, Allamano & Wilson, 1999). Manipulation is accomplished by *the central executive* for attention control, inhibition and temporal order. A further theoretical development includes a fourth component – the episodic buffer that provides temporary storage of information held in a multimodal code (Baddeley, 2000). Another view was suggested by Honig (1978) which

focuses on the continuous taking in new and suppressing old information (see Landrø, Rund, Lund *et al.*, 2001).

Functional neuroimaging studies have shown that working memory is mediated by a distributed neural system that is comprised of multiple, bilateral regions in the anterior and posterior cerebral cortex (Cabeza & Nyberg, 2000). Working memory tasks in general, and particularly tasks that place high demands on executive resources, have been associated with increased neuronal activation in the prefrontal cortex (PFC) (Smith & Jonides, 1999). However, the functional fractionation of the PFC is still a controversial issue. Several models posit that processing in the PFC is organized by material type. It has been proposed that verbal WM is left lateralized (Smith & Jonides, 1999) and a left/right lateralization has been proposed for object WM and spatial WM, respectively (McCarthy, Puce, Constable & Krystal, 1996). According to a model proposed by Goldman-Rakic (1996) processes in the PFC are organized in a dorsal/ventral fashion subserving spatial and object WM, respectively. An alternative model posits organization by type of processes and suggests that a dorsal/ventral subdivision of lateral PFC subserves manipulation and maintenance processes, respectively (Petrides, 1996). In the posterior regions of the brain, on the other hand, there is solid evidence for stimulus specific segregation of activation corresponding to the stimulus dimensions proposed by

Baddeley and Hitch (Cabeza & Nyberg, 2000; Fletcher & Henson, 2001).

Neuroimaging studies of visual working memory have often used face identity as the object to be remembered (Courtney, Ungerleider, Keil & Haxby, 1996, 1997; Haxby, Ungerleider, Horwitz, Rapoport & Grady, 1995; Jaeggi, Seewer, Nirkko *et al.*, 2003; Owen, Stern, Look, Tracey, Rosen & Petrides, 1998; Rama, Sala, Gillen, Pekar & Courtney, 2001). Mixed facial expressions have, however, rarely been studied. Since facial displays always convey an emotional expression, mixing different expressions would control for the potential confounding effects from specific facial characteristics. We used functional magnetic resonance imaging (fMRI) to test the hypothesis that facial characteristics activate specific brain areas not observed in non-facial displays made up of the same visual components as the facial expressions. We thus used drawings of facial expressions contrasted with drawings of the face expressions scrambled, like a "Picasso painting" that were presented in an n-back task. Drawings of facial expressions were used in order to maximize the emotional connotations and minimize the confounding factor of face identity recognition (Magnussen, Sunde & Dyrnes, 1994). Although schematic facial expressions have reduced ecological validity compared to real faces, their visual features can be tightly controlled so as to minimize differences in familiarity, relative differences in similarity, and individual variability between different facial expressions (Oehman, Lundqvist & Esteves, 2001). Moreover, it has been shown that processing of mixed facial emotions activates regions associated with unitary emotions (Critchley, Daly, Phillips *et al.*, 2000). This may suggest a neural network which not only can be associated with transient responses to unitary emotions but also with more state dependent processing, such as monitoring continuously changing facial expression. The aim of the study was thus to investigate the interaction between two such state dependent processes, i.e. working memory and emotional processing. The basic idea was that all stimuli contained the same visual components that were organized in different ways, thus causing the perception of either a facial expression or a scrambled abstract drawing (Hugdahl, Iversen, Ness & Flaten, 1989). By using a variety of different facial expressions with different emotional connotations we thus controlled for any confounding effects of a particular facial display. By mixing the emotional connotations/content, we would thus capture brain areas that are jointly activated by different emotional expressions which would otherwise be undetected. The scrambled faces drawings were used as control stimuli to filter out areas activated by visual and attentive features in the stimuli.

METHOD

Subjects

Twelve right-handed subjects (6 males and 6 females, age 21–29) were recruited from the campuses of the University of Bergen. All

participants were screened for medical, neurological, and psychiatric illnesses. The subjects gave written consent and were paid for participating in the experiment.

Stimuli and procedure

The stimuli were schematic drawings of six different facial expressions taken from Hugdahl *et al.* (1989), and six different scrambled drawings that were constructed for this experiment, see Fig. 1.

The face drawings consisted of a circle with two dots as the eyes, eyebrows and mouth line. The six different facial expressions were created by varying the angle of the eyebrows (V-shaped or Λ -shaped) and the direction of the mouth-line (upward, straight or downward line). The control stimuli were created by scrambling the features in the face circle so that they did not give an impression of a face or a face-like expression. The stimulus presentations were controlled by the Micro Electronic Laboratory (MEL2) software (Psychology Software Tools Inc.). Each stimulus was presented for 1 s followed by a blank inter stimuli interval of 2 s. The stimuli were viewed in specially designed goggles consisting of LCD-screens (Magnetic Resonance Technology Inc.) that were connected to a PC outside the MR chamber which contained the MEL2 software.

The subjects performed an n-back task with three levels within each stimulus category, providing a total of 6 conditions, see Fig. 1. In the 0-back condition, subjects pressed a button to a predetermined target stimulus. In the 1-back condition, they responded when the stimulus matched the previous one. In the 2-back condition, they responded when the stimulus matched the stimulus shown two places back in the sequence. Responses were balanced across conditions so that 33% of stimuli required a motor response. Each condition, or run, was presented in a block, or box-car design consisting of 3 ON and 4 OFF-blocks. There were 18 stimulus presentations in each ON block giving a total of 54 trials per run. The stimulus category was randomized and balanced across subjects and the n-back levels were presented in an increasing order. The OFF-blocks consisted of passive resting with no stimulus presentations and the subject only heard the ambient MR machine noise.

Prior to the MR scanning, the experimental task was demonstrated and instructions were given. Before each condition, the instructions were repeated again in the MR scanner environment. A response button was placed on the subjects' chests that she/he was instructed to press according to the specific instructions for each run. During the initial scanning of anatomy a summary picture of all facial expressions and scrambled drawings were shown in alternating blocks of 30 seconds, to familiarize the subject with the stimuli. After the experiment, the subjects were given a short questionnaire. First they were asked to indicate which stimulus category they experienced as the most difficult. And second they were asked to indicate with a pencil mark on a 6 cm line if they predominantly used a visual or verbal mnemonic strategy for each 1-back and 2-back condition.

fMRI scanning

The fMRI was performed with a 1.5T Simens Vision Plus scanner equipped with 25 mT/m gradients. Initial scanning of anatomy was done with a T1-weighted 3D FLASH pulse sequence. Serial imaging was done with a BOLD sensitive echo planar (EPI) sequence. For the fMRI whole brain EPI scans consisted of 40 contiguous axial slice scans. The MR sequence parameters were: flip angle (FA) 50° acquisition time (TA) 4 s, repetition time (TR) 6, echo time (TE), field of view (FOV) 230 mm, matrix 64 × 64. This yielded a measurement time of 4 s and an in-plane pixel resolution of 3.44 × 3.44 mm. With a slice thickness of 3.0 mm this provided nearly isotropic voxels. The delay period between the end of one volume measurement to the beginning of the next was 2 s. The effective TR-time was thus

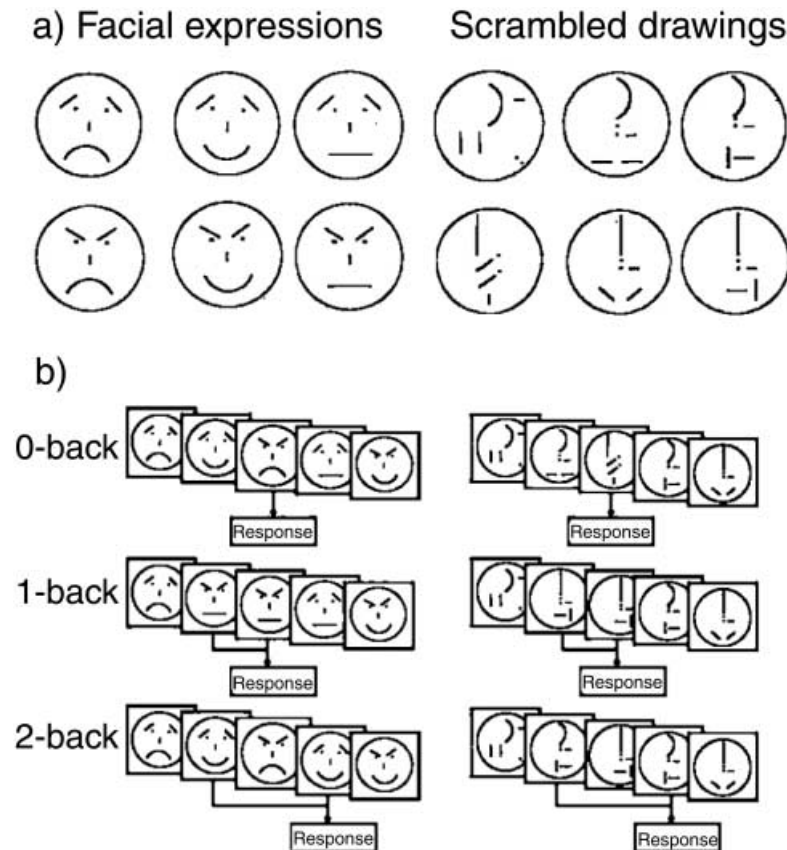


Fig. 1. (a) Shows schematic facial expressions and scrambled drawings used in the n-back task; (b) shows a trial schematic of the n-back task conditions.

6 s. The ON block consisted of 9 EPI scans, and the OFF block consisted of 5 EPI scans. The first OFF block for each run was not used in the statistical analysis, to avoid novelty effects.

Data analysis

The data for the different conditions were modeled according to a “box-car” stimulus function that was convolved with the hemodynamic response function as implemented in the Statistical Parametric Mapping (SPM99) analysis software package (Wellcome Department of Cognitive Neurology, <http://www.fil.ion.ucl.ac.uk>) run under MATLAB (Mathworks, Natick, MA, USA). Statistical analyses were performed using contrasts according to the “General Linear Model” as implemented in the SPM99 package. The EPI-scans were realigned intra-individually to the first image in each time series on a voxel-by-voxel basis to correct for head movements. The realigned images were then coregistered with the 3D-FLASH anatomy images, transformed into the standardized stereotactic reference system developed by Talairach and Tournoux (1988) (MNI version) and smoothed with a 6 mm Gaussian kernel. Effects of whole volume global effects were removed, and the time series data were high-pass filtered to remove artefacts due to cardio-respiratory and other cyclical influences.

Group as well as single subject analyses were performed with the SPM99 software. A linear contrast for memory load was computed for each stimulus type separately for each subject, using a fixed-effects analysis. This means that memory load was weighted linearly corresponding to the increase in processing demands from the 0- to the 1- and to the 2-back condition. The contrast images from the SPM

single subject analysis were then fed into a second-order random-effects analysis to assess group main-effects for memory load, as well as memory load \times stimulus category interactions. Areas with statistically significant changes in signal intensity were determined using the *t*-statistic on a voxel basis. Main effects are reported at $p = 0.05$ corrected and interaction effects are reported at $p < 0.001$, with a minimum of 5 voxels to define a cluster.

Behavioural data were analyzed statistically using an analysis of variance for repeated measures (ANOVA). The mnemonic strategy data were scored in millimeters from left to right. A high score indicates a predominantly visual mnemonic strategy and a low score indicates a verbal strategy. The data were analyzed statistically using an analysis of variance for repeated measures (ANOVA).

RESULTS

Response accuracy was above 85% for all conditions combined with no significant differences between the conditions. Analysis of reaction time (RT) showed a strong trend for the memory load factor $F(1, 10) = 6.78$, ($p = 0.052$). Fisher's Least Significant Difference (LSD) *post-hoc* test showed a significant difference between the 1-back and 2-back conditions, $p = 0.02$, with longer RT in the 2-back task. There was also a strong trend between 0-back and the 2-back tasks ($p = 0.060$).

The results from the questionnaire showed that the facial drawings were considered more difficult to remember by

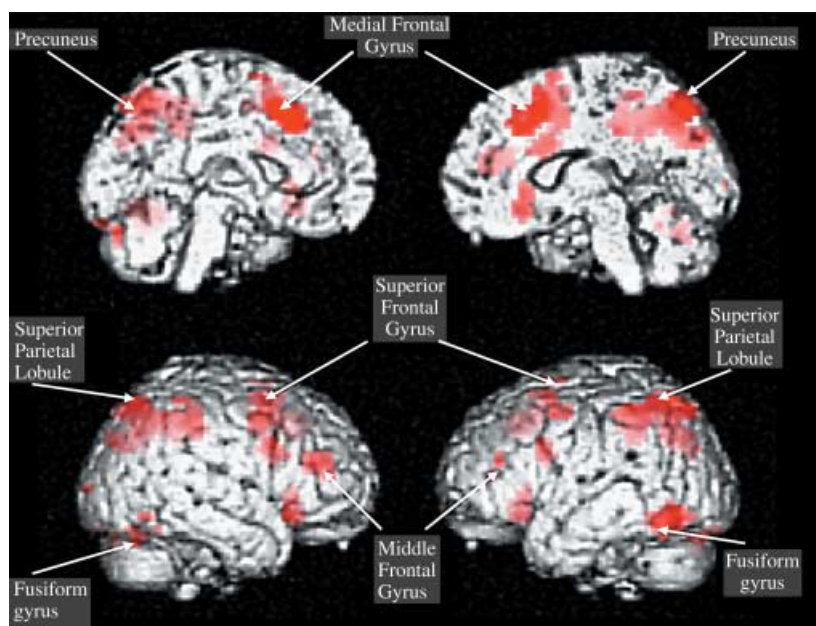


Fig. 2. Renderings of significant activations on a 3D anatomy template during increasing memory load for facial expressions and scrambled drawings. Threshold and other statistical parameters are given in Table 1.

five subjects (3 males and 2 females) whereas seven subjects (3 males and 4 females) considered the scrambled drawings more difficult to remember. Analysis of mnemonic procedure used by the subjects showed a significant effect of gender, $F(1, 10) = 11.89$, $p < 0.01$, where females tended to use a more verbal strategy and the males a more visual strategy. There was also a significant effect of strategy $F(1, 10) = 5.47$, $p < 0.01$, indicating that a verbal strategy was predominantly used for the facial expressions and a visual strategy was predominantly used for scrambled drawings.

A linear weighted parametric contrast was used to reveal brain regions that showed gradually increasing signal intensity as a function of increasing working memory load. An increase in BOLD signal intensity with increasing memory load was found bilaterally in the fusiform gyrus, the precuneus, the superior parietal lobe, the insula, the middle and superior frontal gyrus, and the cerebellum. The same was also found in the left inferior frontal gyrus and the medial frontal gyrus, and the right middle occipital gyrus. The corresponding significant activations of the main effect of memory load are rendered on the SPM template brain and are shown in Fig. 2 together with the corresponding MNI coordinates anatomical localizations and Z- and p -values presented in Table 1.

The memory load \times stimulus category interaction caused activations in the right inferior frontal gyrus in favor of facial expressions. The reverse comparison did not yield any significant activation. The anatomical localizations and the MNI coordinates for peak voxels are shown in Table 1. The corresponding significant activations rendered on the SPM template brain are shown in Fig. 3.

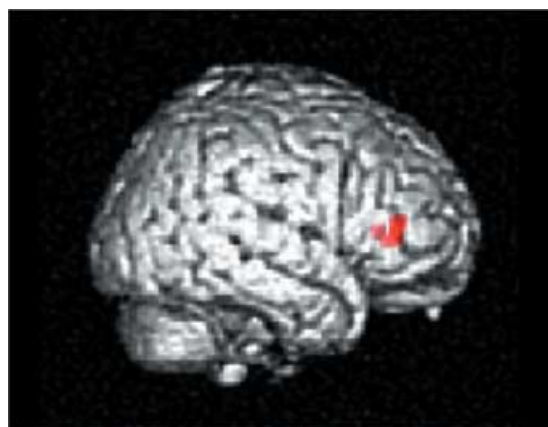


Fig. 3. Renderings of significant activations on a 3D anatomy template of facial expressions > scrambled drawings comparison during increasing memory load. Threshold and other statistical parameters are given in Table 1.

DISCUSSION

We found that performance in a parametric working memory task with two different categories of visual stimuli yielded activations in a bilaterally distributed cortical network consisting of regions in the occipitotemporal cortex, the inferior parietal lobule, the dorsolateral prefrontal cortex (DLPFC), supplementary motor area (SMA) and the cerebellum. The cerebral activations are in agreement with other working memory studies that have used faces (Druzgal & D'Esposito, 2001; Rama, Sala, Gillen *et al.*, 2001), and stimuli with

Table 1. Stereotactic locations of areas of significantly greater activation for the n-back main effect ($p = 0.05$ corrected) and the facial expressions – scrambled drawings interaction effect ($p < 0.001$ uncorrected, 5 voxel extent threshold)

	Coordinates					
Anatomical localization	x	y	z	Cluster	Z-value	p-value
<i>n-back main effect</i>						
Left fusiform gyrus, BA 37	-44	-55	-11	47	7.03	<0.001
Right precuneus, BA 7	24	-52	43	188	6.90	<0.001
Left medial frontal gyrus, BA 8	0	21	43	76	6.53	<0.001
Left superior parietal lobule, BA 7	-28	-56	51	164	6.49	<0.001
Right middle frontal gyrus, BA 10/46	40	40	20	34	6.30	<0.001
Right claustrum	28	24	0	28	6.10	<0.001
Right middle/superior frontal gyrus, BA 6	28	7	55	109	6.08	<0.001
Left cerebellum, posterior lobe	-8	-79	-20	6	5.77	=0.001
Left middle frontal gyrus, BA 6	-44	6	44	18	5.73	=0.001
Left insula	-32	23	-1	17	5.72	=0.001
Right cerebellum, posterior lobe	40	-67	-17	7	5.44	=0.001
Left middle frontal gyrus, BA 46	-40	36	17	3	5.44	=0.001
Left inferior frontal gyrus, BA 9	-44	9	25	15	5.32	=0.001
Right superior frontal gyrus, BA 6	4	11	62	3	5.27	=0.001
Right middle occipital gyrus, BA 19	48	-59	-7	3	5.02	=0.005
Left medial frontal gyrus, BA 6	-8	3	62	2	4.88	=0.011
Left inferior occipital gyrus, BA 18	-32	-83	-16	2	4.80	=0.016
Right cerebellum, posterior lobe	4	-79	-16	1	4.77	=0.018
Left fusiform gyrus, BA 19	-36	-75	-16	1	4.76	=0.019
Right fusiform gyrus, BA 37	44	-55	-14	1	4.76	=0.020
Left middle frontal gyrus, BA 10	-40	39	9	1	4.72	=0.024
Left fusiform gyrus, BA 18	-20	-86	-13	2	4.63	=0.037
Right middle occipital gyrus, BA 18	28	-92	4	1	4.61	=0.039
Left middle frontal gyrus, BA 6	-28	6	44	1	4.58	=0.047
<i>Facial expressions > scrambled drawings</i>						
Right inferior frontal gyrus, BA 47	40	35	2	7	3.57	<0.001*

* uncorrected.

emotional connotations (Rama, Martinkauppi, Linnankoski *et al.*, 2001). The n-back task loads heavily on both maintenance and manipulation processes, and the activations in the DLPFC are therefore in agreement with a process-specific model of working memory (Petrides, 1996). The process-specific model postulates that executive processes are implemented in the DLPFC, as opposed to a domain-specific model which suggests that the DLPFC is associated with maintenance and manipulation of visuospatial information (Goldman-Rakic, 1996). This would also be in agreement with the findings by Landrø *et al.* (2001), who used a slightly different working memory paradigm.

There was a memory load \times stimulus interaction in the right inferior frontal gyrus, BA 47. Activation in this region was enhanced while mixed facial expressions were maintained in working memory compared to scrambled drawings. The right hemisphere and the inferior prefrontal cortex have previously been associated with both processing of face identity (Haxby *et al.*, 1995) and different facial expressions (Nakamura, Kawashima, Ito *et al.*, 1999). A difference between schematic facial expressions and scrambled drawings could be due to a verbal recoding strategy, as it was reported by the subjects. But this explanation is less plausible since

the activation was right lateralized. It may therefore be reasonable that the working memory activity in the right inferior prefrontal gyrus was modulated by differences in the stimuli's connotations. Perlstein, Elbert and Stenger (2002) reported that working memory processing in the PFC is influenced by stimuli's emotional connotations, which was enhanced by pleasant and reduced by unpleasant stimuli. The location of the peak voxel did not overlap with activations seen for the memory load main-effects. According to Gray, Braver and Raichle (2002) the existence of interaction effects in a region with no main effects of either stimulus or memory load could mean that different processes are integrated and that at some point in the processing chain functional specialization is lost.

Our findings support a process-specific organization of the PFC but the results also show that a region in the right inferior frontal gyrus was sensitive to a distinction that focuses on the face characteristics of the stimuli. Activation in this region was enhanced while mixed facial expressions were maintained in working memory compared with the scrambled drawings. It could be that working memory processing in the PFC is influenced by the processing of mixed emotional connotations or that the activated region

represents an integration of working memory and emotional processing. Further studies are needed to resolve these questions, but the findings nevertheless suggest that the organization of working memory in the PFC should take into consideration connotative parameters.

The present research was financially supported by grants to Kenneth Hugdahl from the Research Council of Norway and Helse-Vest, Bergen.

REFERENCES

- Baddeley, A. (2000). The episodic buffer: A new component of working memory? *Trends in Cognitive Sciences*, 4(11), 417–423.
- Baddeley, A. (2003). Working memory: Looking back and looking forward. *Nature reviews. Neuroscience*, 4(10), 829–839.
- Cabeza, R. & Nyberg, L. (2000). Imaging cognition II: An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience*, 12(1), 1–47.
- Courtney, S. M., Ungerleider, L. G., Keil, K. & Haxby, J. V. (1996). Object and spatial visual working memory activate separate neural systems in human cortex. *Cerebral Cortex*, 6(1), 39–49.
- Courtney, S. M., Ungerleider, L. G., Keil, K. & Haxby, J. V. (1997). Transient and sustained activity in a distributed neural system for human working memory. *Nature*, 386(6625), 608–611.
- Critchley, H., Daly, E., Phillips, M., Brammer, M., Bullmore, E., Williams, S., et al. (2000). Explicit and implicit neural mechanisms for processing of social information from facial expressions: A functional magnetic resonance imaging study. *Human Brain Mapping*, 9(2), 93–105.
- Darling, S., Della Sala, S., Logie, R. H. & Cantagallo, A. (2006). Neuropsychological evidence for separating components of visuospatial working memory. *Journal of Neurology*, 253(7), 176–180.
- Della Sala, S., Gray, C., Baddeley, A., Allamano, N. & Wilson, L. (1999). Pattern span: a tool for unwinding visuo-spatial memory. *Neuropsychologia*, 37(10), 1189–1199.
- Druzgal, T. J. & D'Esposito, M. (2001). Activity in fusiform face area modulated as a function of working memory load. *Cognitive Brain Research*, 10(3), 355–364.
- Fletcher, P. C. & Henson, R. N. A. (2001). Frontal lobes and human memory: Insights from functional neuroimaging. *Brain*, 124(5), 849–881.
- Goldman-Rakic, P. S. (1996). Regional and cellular fractionation of working memory. *PNAS*, 93(24), 13473–13480.
- Gray, J. R., Braver, T. S. & Raichle, M. E. (2002). Integration of emotion and cognition in the lateral prefrontal cortex. *PNAS*, 99(6), 4115–4120.
- Haxby, J. V., Ungerleider, L. G., Horwitz, B., Rapoport, S. I. & Grady, C. L. (1995). Hemispheric differences in neural systems for face working memory: A PET-rCBF study. *Human Brain Mapping*, 3(2), 68–82.
- Honig, W. K. (1978). Studies of working memory in the pigeon. In S. H. Hulse, H. Fowler & W. K. Honig (Eds.), *Cognitive processes in animal behavior* (pp. 211–248). Hillsdale, N.J.: Lawrence Erlbaum Associates.
- Hugdahl, K., Iversen, P. M., Ness, H. M. & Flaten, M. A. (1989). Hemisphere differences in recognition of facial expressions: A VHF-study of negative, positive, and neutral emotions. *International Journal of Neuroscience*, 45, 205–213.
- Jaeggi, S. M., Seewer, R., Nirkko, A. C., Eckstein, D., Schroth, G., Groner, R., et al. (2003). Does excessive memory load attenuate activation in the prefrontal cortex? Load-dependent processing in single and dual tasks: functional magnetic resonance imaging study. *NeuroImage*, 19(2), 210–225.
- Landrø, N. I., Rund, B. R., Lund, A., Sundet, K., Mjellem, N., Asbjørnsen, A., et al. (2001). Honig's model of working memory and brain activation: An fMRI study. *NeuroReport*, 12, 4047–4054.
- Magnussen, S., Sunde, B. & Dyrnes, S. (1994). Patterns of perceptual asymmetry in processing facial expression. *Cortex*, 30(2), 215–229.
- McCarthy, G., Puce, A., Constable, R. T. & Krystal, J. H. (1996). Activation of human prefrontal cortex during spatial and non-spatial working memory tasks measured by functional MRI. *Cerebral Cortex*, 6(4), 600–611.
- Nakamura, K., Kawashima, R., Ito, K., Sugiura, M., Kato, T., Nakamura, A., et al. (1999). Activation of the right inferior frontal cortex during assessment of facial emotion. *Journal of neurophysiology*, 82(3), 1610–1614.
- Oehman, A., Lundqvist, D. & Esteves, F. (2001). The face in the crowd revisited: A threat advantage with schematic stimuli. *Journal of Personality and Social Psychology*, 80(3), 381–396.
- Owen, A. M., Stern, C. E., Look, R. B., Tracey, I., Rosen, B. R. & Petrides, M. (1998). Functional organization of spatial and non-spatial working memory processing within the human lateral frontal cortex. *Proceedings of the National Academy of Sciences of the United States of America*, 95(13), 7721–7726.
- Perlstein, W. M., Elbert, T. & Stenger, V. A. (2002). Dissociation in human prefrontal cortex of affective influences on working memory-related activity. *PNAS*, 99(3), 1736–1741.
- Petrides, M. (1996). Specialized systems for the processing of mnemonic information within the primate frontal cortex. *Philosophical transactions of the Royal Society of London. Series B Biological sciences*, 351(1346), 1455–1461; discussion 1461–1452.
- Rama, P., Martinkauppi, S., Linnankoski, I., Koivisto, J., Aronen, H. J. & Carlson, S. (2001). Working Memory of Identification of Emotional Vocal Expressions: An fMRI Study. *NeuroImage*, 13(6), 1090–1101.
- Rama, P., Sala, J. B., Gillen, J. S., Pekar, J. J. & Courtney, S. M. (2001). Dissociation of the neural systems for working memory maintenance of verbal and nonspatial visual information. *J(2)*, 161–171.
- Smith, E. E. & Jonides, J. (1999). Storage and Executive Processes in the Frontal Lobes. *Science*, 283, 1657–1661.
- Talairach, J. & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain, 3-D proportional system: An approach to cerebral imaging*. Stuttgart and New York: Georg Thieme Verlag.

Received 20 June 2005, accepted 14 November 2005