Conscious perception of visual objects: The role of premotor cortex

M. S. Christensen[1,2], K. H. Madsen[1,2], K. Sidaros[1], T. Lund[1], R. Cotterill[2]

[1]Danish Research Centre for Magnetic Resonance, Hvidovre, Denmark, [2]Technical University of Denmark, Lyngby, Denmark

Introduction

Essentially since the time of Aristotle, human consciousness has been regarded as being passively generated by incoming stimuli. This view is not supported by the present study. It will indicate that consciousness is associated with covert (imagined) movements operating below the threshold for overt (observable) movement. Hence the focus of this study is on the movement preparation areas of the brain. The present study investigates visual object perception using event related fMRI, without direct correlation between object perception and the behavioural report of key presses. We have also found several cortical and subcortical areas involved in key presses.

Theory

In principle the only external product on ms timescale of the central nervous system's activity is muscle contractions. The cerebellum, basal ganglia, and anterior cingulate cortex can veto muscle contractions, and prevent signals from the sensory cortices from exceeding the threshold for overt movement. The premotor (PMC) and supplementary motor (SMC) cortices provide the necessary patterns for motor output. But these can be vetoed by the above-mentioned areas. Signals from the PMC/SMC make several loops through the anterior cingulate cortex, the intralaminar nuclei of the thalamus, and the sensory cortices. These signalling routes indicate that consciousness arises through a mechanism that is the antithesis of the one invoked by the stimulus-response paradigm, as suggested by R. Cotterill [1].

Methods

MR scan: 14 healthy (7 f.) right-handed subjects were scanned in a Siemens 3T Magnetom Trio scanner, using a gradient echo EPI sequence, TR = 2400 ms, TE = 30 ms, 64x64 matrix. Each session consisted of 400 whole brain volume scans of 40 slices, with a voxel size of 3x3x3mm^3. Total scan time was 960 s.

Visual stimuli: 16 different non-figurative objects were superimposed on a random dotted grey-scale background. These being displayed 4 times in random order interleaved by 16 null events (random dotted grey scale background). The intensity of the figures was gradually increased to a maximum and then decreased, in all lasting 12 s. The increase and decrease of the stimuli intensity was asymmetric, in this way large variations in time of press only lead to small variations in modelled time of perception (see Fig. 1).

Task: Subjects were instructed to press a key when they stopped seeing the object. They were instructed to switch between pressing the right and left index finger.

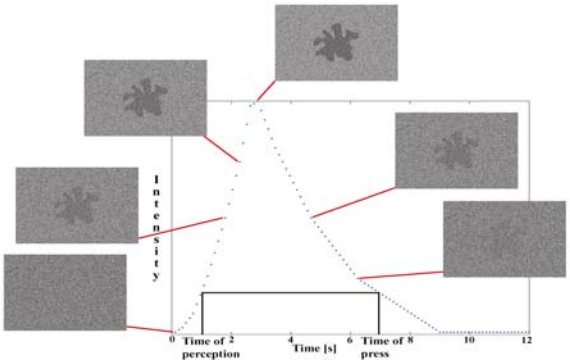

Fig. 1: Intensity variation of visual stimuli

Analysis

All data were analysed using SPM2 (http://www.fil.ion.ucl.ac.uk/spm). All data were normalised to a standard EPI template, and smoothed with a Gaussian kernel (FWHM=8 mm). Four events were modelled for each subject. Two press events, i.e. the times at which they had pressed either the left or the right index finger key in order to indicate that they did not perceive the object any more (press left, press right). These two perception events were modelled, depending on whether the subject afterwards had pressed the left or right index finger (perception left and perception right). The two perception events were modelled on the basis of the intensity of the figure at the time of the key press (see Fig. 1). The regressors were convolved with a canonical hemodynamic response function and serial correlations were modelled using an AR(1) model. A high-pass filter with a cut-off of 128 ms was used. A one-way Anova test was used at 2nd level of analysis, with the four event types as groups, corrected for correlations between the four images (one image per event type) from the same subject. Responses were considered significant at $P<0.05$ using False Discovery Rate correction [2]. The activity shared between the two perception events is either correlated with perception of the visual objects or involved in a generalised motor preparation for both left hand and right hand key presses.

Results

Substantial activity was shared in the two perception events (blue) vs. baseline in the fusiform gyrus of both the occipital and the temporal lobe (l. & r.) (Fig. 8), in the superior parietal lobe (l. & r.) (Fig. 7, Fig. 8), in the ventral part of the precentral gyrus (l. & r.)(ventral PMC, extending into BA 44 in r. hand side) (Fig. 2, Fig. 3), in the superior frontal gyrus, and in the cingulate gyrus. There was different activity in the left (green) and right (red) perception events in the precentral gyrus (M1) (Fig. 3, Fig. 4), in the medial SMC (Fig. 3, Fig. 4), in the ventrolateral (vl.) nucleus of the thalamus (Fig. 4, Fig. 5), and in insula (Fig. 4), in the contralateral side of the forthcoming key press. Activity was also found and in the ipsilateral side to forthcoming key press in the dentate nucleus of cerebellum (Fig. 6, Fig. 7).

Discussion

The widespread activity in the fusiform gyrus is probably found due to the "object" character of the visual stimuli. The activity in parietal lobe could be caused by the similarity of the stimulus presentation to movement. The activity that changes depending on which finger to use, is either correlated with motor preparation or motor execution of the forthcoming key press. The latter would be explained by a faster hemodynamic response in the primary motor cortex, which seems to be the case because a canonical hemodynamic response function is used, hence activity stemming from the key press event has been modelled in the perception event [3]. Activity in the medial frontal gyrus has also been found to underlie finger movement preparation independent of which hand to move [4]. Dependent on which finger to move the activity in SMC is very well distributed between the two hemispheres, and is involved in preparation of the key press. The activity in thalamus is probably present along with the activity in the cerebellum due to early involvement in motor execution, and is therefore modelled in the perception event. Insular activity is rarely found correlated with motor activity, but has been suggested to serve as a feed-forward control of cardiovascular regulation during motor activity [5]. We believe the activity in vPMC, in the anterior cingulate gyrus, and in the visual cortex together form a network of activities underlying consciousness. Activity in vPMC along with activity in the fusiform gyrus has been found to change during conscious perceptual shifts in binocular rivalry [6]. This present study together with the binocular rivalry study supports a theory of consciousness as being covert movements operating below a threshold for overt movement. This study is also an experimental verification using fMRI of the early involvement of the vl. nucleus of the thalamus and the dentate nucleus of the cerebellum in motor execution.

References

[1] Cotterill (2001) *Progress in Neurobiology* 64:1-33, **[2]** Genovese et al. (2002) *NeuroImage* 15:870-878 **[3]** Birn et al. (2001) *NeuroImage* 14:817-826, **[4]** Joliot et al. (1999) *NeuroImage* 10:430-447, **[5]** Nowak et al. (1999) *J. Appl. Physiol* 86(3):819-824, **[6]** Lumer, Rees (1999) *Proc. Natl. Acad. Sci. USA* 96:1669-1673

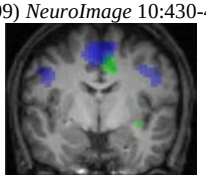

Fig. 2: y = -2

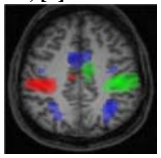

Fig. 3: z = 50

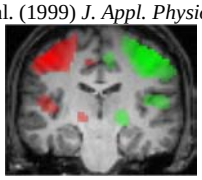

Fig. 4: y = -22

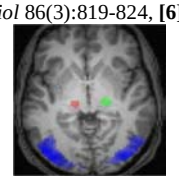

Fig. 5: z = 1

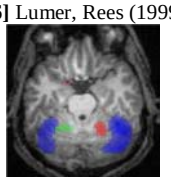

Fig. 6: z = -22

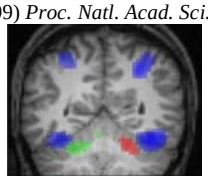

Fig. 7: y = -50

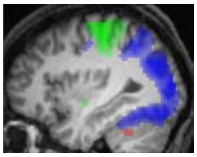

Fig. 8: x = 21