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Drawing cartoon faces – a functional imaging study of the cognitive neuroscience of drawing

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Abstract

We report a functional imaging study of drawing cartoon faces. Normal, untrained participants were scanned while viewing simple black and white cartoon line-drawings of human faces, retaining them for a short memory interval, and then drawing them without vision of their hand or the paper. Specific encoding and retention of information about the faces was tested for by contrasting these two stages (with display of cartoon faces) against the exploration and retention of random dot stimuli. Drawing was contrasted between conditions in which only memory of a previously viewed face was available versus a condition in which both memory and simultaneous viewing of the cartoon was possible, and versus drawing of a new, previously unseen, face. We show that the encoding of cartoon faces powerfully activates the face sensitive areas of the lateral occipital cortex and the fusiform gyrus, but there is no significant activation in these areas during the retention interval. Activity in both areas was also high when drawing the displayed cartoons. Drawing from memory activates areas in posterior parietal cortex and frontal areas. This activity is consistent with the encoding and retention of the spatial information about the face to be drawn as a visuo-motor action plan, either representing a series of targets for ocular fixation or as spatial targets for the drawing action.

Keywords: functional imaging; face processing; spatial processing; visuo-motor control; spatial memory

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Introduction

Drawing is a complex voluntary visuo-motor task that is performed by most adults, even if rather infrequently. In most people it is a stable long-maintained skill, with little or no active learning component, because we typically learn to draw during childhood and rarely try to improve in later life. Drawing therefore represents an interesting cognitive task to understand, and can be readily studied in the laboratory or in a functional brain scanner.

Drawing also comprises a number of key cognitive processes that are still poorly understood. These can be functionally divided into the processes necessary to capture the target visual image, hold this in memory while transferring gaze and the pencil to the paper, execute of a drawing action, and visually inspect the drawn line. Our aim is to understand these steps in more detail. First the object to be drawn must be examined and decisions made about what features are to be drawn. For an artist drawing a face from life, this can be a highly complex decision process, as there are few clear contours or boundaries on the face other than, as examples, the hairline around the forehead, or the edges of the eyes or mouth. Hence the graded changes in depth, texture or contrast around the nose, for example, must be abstracted from the image on the retina. This decision process leads to selection of a few carefully chosen lines, which when drawn by a skilful artist can beautifully capture a likeness (Miall and Tchalenko 2001), or can exaggerate features to aid identification (Benson and Perrett 1994). The decisions about what to draw will change as the drawing progresses, so that at a trivial level features already drawn once are not duplicated. But at a more complex level, the judgements about what lines remain to be drawn are likely to be based on how the drawing is evolving, with new lines being chosen to compliment those already drawn, or so that drawn lines may be strengthened, extended or erased to ensure the likeness is captured well.

Second, there must be a mental retention of the chosen features in some form, even if only for a few seconds, as the artist looks away from the model's face to the paper and executes the next stage of drawing. It is not clear what form of representation might be used at the stage. Possibilities are that a mental visual image of the whole face or of a selected feature is retained,

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perhaps by maintaining ongoing activity within the brain's visual processing areas. Previous functional imaging work has shown that when visual imagery is employed, there is activation of primary and secondary visual cortical areas (Chen et al. 1998b; Ganis et al. 2004b; Ishai et al. 2002a; O'Craven and Kanwisher 2000b). However, it may be that the short term memory is spatial rather than visual (Graziano and Gross 1998; Kakei et al. 2003). For example, it may be stored as one or more allocentric locations with respect to the rest of the scene or with respect to the progressing drawing on the page. These spatial locations might be used as reference positions for the planned line on the paper, and might include higher level abstractions such as some representation of the desired line length, orientation, curvature etc (De Winter and Wagemans 2006; Flanders et al. 2006a). Alternatively, it is possible that the information is stored as a motor plan, either encoded as future fixation points for the eyes or of the required hand action to produce the chosen line on the paper (Snyder 2000). This representation would also include spatial locations, but would be expected to be held within areas of the brain closely coupled to the voluntary control of eye and/or hand (Jeannerod and Decety 1995; Sirigu and Duhamel 2001).

Finally, having chosen the line and its position, the artist executes the drawing on the paper, and in normal drawing conditions would use visual, proprioceptive and haptic signals to carefully guide the pencil's motion, so that each new line adds a small piece to the developing drawing. The artist then either returns their gaze to the model to capture further features, or examines the drawing to monitor its progress before returning to the model. This cycle continues until the drawing is complete (Konecni 1991; Miall and Tchalenko 2001; Tchalenko et al. 2003).

The aim of this paper is to decompose the drawing process into these separate steps (visual encoding, memory, and execution), and to record the functional activity in the brain during their performance. To simplify the task, and to allow easier comparisons with other brain-imaging studies, we have studied the copying of simple line drawings of cartoon faces by participants who are untrained in fine drawing. The cartoon faces were displayed on a screen in front of the eyes, but participants had no direct vision of either the paper or the pencil in their hands, allowing us to separate out the process of visual capture of the image from visual guidance of the hand. We

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also separated the task into discrete blocks, with stages of visual encoding, memory and execution, so that standard block analyses of the functional data were possible. Finally, we challenged the participants to draw from memory in one condition, to directly copy without memory in another, and we allowed both memory and vision in a third condition, in order to test for functional differences in activity if the drawing is executed with or without memory. This design also allowed us to direct test the memory stage by comparing functional activation during a memory interval after viewing a face against an interval without memory of a cartoon face.

Methods

Participants

Thirteen subjects including the authors RCM and EG took part in this study, after giving written informed consent. The study was approved by our local ethical review board and complied with the Declaration of Helsinki. Subject ages ranged from 18 to 50; 8 were male, and all were right-handed. None of the subjects reported any unusual history of drawing, and they were not selected for drawing ability.

The task involved viewing black and white line drawings of cartoon faces in profile (Figure 1), and drawing these faces on a hand held pad of paper using a short graphite pencil. The visual display screen was vertically positioned behind the subject's head, viewed in a rear-view mirror with a viewing distance of approximately 60 cm, and subtended a horizontal and vertical visual angle of approximately 25x20 degrees. Subjects held the drawing pad with their left hand, partly supported on a pillow across their lap, but were not able to view the pad or pencil.

A remote eye-tracker (ASL-504) was used to record left eye gaze position in 6 subjects but due to technical difficulties good quality gaze position was only available for 4 subjects. Limited analysis of the eye records have been attempted, mainly to confirm fixation during the required periods. Qualitative description of eye movement for all 6 subjects was possible during scanning by

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observing either the image from the eye-camera or from the scene camera, which showed the gaze position superimposed as a cursor on an image of the display screen.

FIGURE 1 NEAR HERE

Tasks

The experiment consisted of a block design with 8 different conditions which comprised a matrix of 3 different trial types and five blocks within each trial (Figure 2). The main design used two different encoding conditions (with or without a cartoon face to encode) and hence two subsequent retention conditions, but we included three drawing conditions in order to test drawing from memory without an on-screen image, drawing a new face without memory and a combination of these consisting of drawing a memorised face that was redisplayed on-screen. All trials had a common page turning condition. When presented as series of 5 related conditions, these constituted three different tasks, namely to draw a newly seen face without prior encoding to memory (NewDraw; Figure 2A), to encode and draw a cartoon face when seeing the face during encoding and drawing (CombinedDraw, Figure 2B), and to encode a face but draw it from memory (MemoryDraw, Figure 2C). Instruction cues about each block were provided on screen, just above the visual stimuli. The first block in each trial was a control or baseline condition designed to block visual imagery of any previously viewed faces and to block any rehearsal of face drawing; we have therefore used a challenging high-level baseline rather than the more common low-level resting baseline. As the functional activation in all the conditions of interest was measured relative to this baseline, we expect in some conditions some areas would have activity lower than the baseline. This is not to be interpreted as negative or inhibitory activity, but simply as lesser activation than in the deliberately cognitively challenging baseline condition. Hence in the baseline “Subtract” condition, two 4-digit random numbers between 1000 and 9999 were presented on screen, the greater number above the smaller one, and participants were instructed by the cue “*Subtract*” to mentally subtract the smaller from the larger (Figure 2i). After 9

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seconds, the screen was replaced by the cue phrase "*Turn page and answer*", and they were instructed to attempt to write as much of the answer as they had calculated (Figure 2ii). This condition was necessary both to confirm that they were attempting the mental arithmetic, and was to provide the next blank page of the book, but is not of further interest. We define it as a separate condition to allow separation of the functional activity involved in the motor actions of turning the page and preparing the pencil from the previous mental arithmetic and from the subsequent face encoding and drawing tasks. After a further 6 seconds, the screen was replaced with either a cartoon face or by 39 randomly positioned black dots, and the cue words "*Encode*" or "*Explore*" respectively. Subjects were instructed to visually explore either image, with the intention to memorize the face for later drawing, or to gaze at each of the randomly positioned dots. Pilot studies in the laboratory had suggested that subjects typically made 2.6 fixations per second when encoding these faces for drawing, so the 39 dots ensured approximately equal numbers of fixations in both conditions. After 15 seconds, the screen was replaced with the single central cue "*Fixate*", and subjects were instructed to fix their gaze on this word. This fixation period was designed as a short-term retention interval, in which the information about the viewed face was retained for subsequent drawing. Note that in both MemoryDraw and in CombinedDraw, the subjects were aware that the remembered cartoon was to be drawn, but they did not know whether or not it would be redisplayed on screen which only happened in CombinedDraw. After a further 15 seconds, the screen was replaced with either the same cartoon as previously displayed (CombinedDraw), with a new, unseen, cartoon (NewDraw), or with a new set of 39 random dots (MemoryDraw), with the on-screen instruction "*Draw*". They were instructed to carefully draw the face, using the full 15s to complete the drawing, and would therefore either draw the same cartoon seen in the previous encoding stage and now redisplayed on screen (CombinedDraw), draw the previously encoded face while only seeing a set of random dots (drawing from memory, MemoryDraw), or draw a new face not seen before, having previously seen only the random dots (drawing without memory, NewDraw). These three drawing conditions were pseudo-randomly ordered and counterbalanced across subjects. The combined condition (drawing a previously encoded and currently redisplayed face) had been included to test for graded memory-dependent

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activation across the three tasks, but as this was not evident, this condition is not reported in any detail in the current work.

Before scanning, participants were given a printed sheet of instruction, and were trained in all conditions lying within a mock scanner of identical bore size to the MR scanner, and with an identical head coil, mirror, projection screen and support of their drawing pad. Verbal instruction was also given in the mock scanner, at the start of this practise session, as they went through the first one or two blocks of stimuli. Practise took 15 minutes, and used a set of left profiles of cartoon faces not used in the main experiment. In the main experiment a different set of cartoon faces were shown in right profile. After practise, subjects were then prepared for the main experiment, and two scanning runs were performed, each of 15 minutes duration. The sets of cartoon faces for each of the two runs were again different.

Scanning protocol

Functional MR imaging used a 3T Philips Achieva with 8-channel parallel head-coil and a Sense factor of 2.0. Fast echo planar T2*-weighted images were acquired with 49 interleaved axial slices and an acquisition matrix of 96 x 96 voxels (FOV=240×240×147mm) with each voxel subtending 2.5x2.5x3 mm (TE=35ms, flip angle=85, TR=3.0s). After 4 dummy volumes, 360 volumes were acquired with scan duration of 18 minutes. The subject was then questioned to ensure task compliance, the pad of paper was replaced with a new pad, and the second scan was begun. Afterwards, a high resolution sagittal orientation 1x1x2 mm T1-weighted structural image was acquired in 4.5 minutes, and then the subject was brought out of the scanner and debriefed.

Data analysis

The functional data were analysed in Feat v5.64, using the FSL software library from FMRIB, Oxford (http://www.fmrib.ox.ac.uk/fsl). The initial four dummy volumes of each functional data

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collection run were discarded to ensure T1 saturation had been achieved. Next, slice timing was corrected and the functional image series was motion corrected to the middle image of the set, using the MCFLIRT linear registration algorithm. Mean head motion with respect the reference image, averaged across all voxels, ranged from 0.22-1.02 mm (median 0.45 mm, n=26). The 6 dimensional motion correction parameters calculated by MCFLIRT were saved to be used as additional covariates within the GLM model. The data were then filtered with a spatial low-pass filter using a Gaussian kernel with 5mm FWHM, and a Gaussian-weighted high-pass filter with a 100s window. Next the brain was extracted from the structural image using the automatic brain extraction tool (BET), in order to register the functional data to the MNI-152 standard image, with 7 DoF affine transform between the average functional image and the structural image, and a 12 DoF affine transform between the structural image and the MNI standard.

A GLM model was constructed using 8 explanatory variables (EVs) and the 6 motion parameters of no interest which were orthogonalized with respect to one another and all other EVs. The EVs represented the 8 conditions firstly: TurnPage (EV1), and the 7 conditions of interest, EncodeFace (EV2), ExploreDots (EV3), RetainFace (EV4), RetainDots (EV5), MemoryDraw (EV6), NewDraw (EV8), and CombinedDraw (drawing a displayed face that was previously encoded into memory, EV7). The mental arithmetic condition (Subtract) was the un-modelled baseline. The 8 EVs and their time derivatives were convolved with a gamma-derived haemodynamic response function (standard deviation of 3s, mean lag of 6s); the 6 motion EVs were not convolved. Within each individual functional imaging session, contrasts testing the relative activation of encoding faces versus exploring dots (EV2 – EV3), remembering faces versus dots (EV4 – EV5), and the activation of all three drawing conditions were calculated (EV6, EV7, EV8 versus baseline). In addition drawing from memory was contrasted with drawing without memory (EV6 – EV8) and visa versa (EV8 – EV6).

At the second level of the analysis, contrasts from all 26 first level analyses were combined using FLAME (FMRIB's Local Analysis of Mixed Effects) stage 1 only (i.e., without the final MCMC-based stage) (Beckmann et al. 2003; Woolrich et al. 2004). Z (Gaussianised T/F) statistic images were thresholded using clusters determined by Z>2.3 and a (corrected) cluster significance

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threshold of P=0.05 (Worsley et al. 1992). Conjunctions of the two drawing contrasts (EV6 – EV8 and visa versa) with the encoding of faces contrast
(EV2 – EV3) were achieved by calculating the geometric mean of the two cluster-thresholded z-statistic maps.

Identification of the anatomical location of clusters used comparisons between the AAL (Tzourio-Mazoyer et al. 2002) voxel labelled atlas, the Brodmann voxel-labelled atlas from MRIcro (http://www.sph.sc.edu/comd/rorden/mricro.html) and two neuro-anatomical reference atlases (Duvernoy 1999; Schmahmann et al. 2000). Group average activation levels for the local maxima within these clusters were compared across the 8 active conditions using the Featquery tool (FMRIB, Oxford). Target voxels were identified as those of highest statistical significance observed in the mean group data of specific contrasts between conditions, or of contrasts of individual drawing conditions against baseline; Featquery then inverts the transformation used to register each individual's brain into the MNI standard space in order to locate the coordinates within the individual brain corresponding to the target coordinate from the group average, and determines the mean parameter estimate (percentage change in BOLD signal) across all subjects and both sessions for each subject.

Results

Overall performance

All subjects correctly performed all conditions. Following each scanning session, the drawing pads were recovered from the subjects, and checked for completion of the drawings in relation to the instructed series. We also checked that they had attempted an answer to each subtraction question. There were considerable between-subject differences in the accuracy of answers, but there were no missing attempts. We cannot easily identify if or when the subjects were fatigued, but we found no overt evidence that their performance of any parts of the tasks were affected by fatigue. We visually inspected the head motion parameters, and found little evidence of greater

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movement as the experiment progressed. Finally, subjectively, the later drawings appeared to be as complete at the end of the experiments as the earlier ones.

Eye movement

Detailed analysis of the gaze path, temporal pattern of fixations and the hand's drawing movements made during these tasks is provided in the accompanying paper (Tchalenko and Miall 2007). In that study participants performed closely related tasks involving direct copying of the same the cartoon faces and viewing the faces both for a recognition task and for a retention task requiring subsequent reproduction of the drawing. The data for the latter condition are still under analysis. In Figure 3 we show the same face viewed and drawn by two subjects, one in the fMRI scanner and one in the laboratory. The pattern of fixations is remarkably similar, and we saw qualitative similarities in most cases. Hence we suggest that the overall pattern of eye movements was little different between the fMRI scan sessions and the laboratory sessions.

All subjects whose eye movements were monitored maintained fixation during the retentions interval, as requested. Numbers of saccades made during encoding of faces and during exploration of the random dots was, as intended, equivalent. However, numbers of saccades made in the three drawing conditions were unbalanced. When drawing from memory, with random dots on the screen, they tended to make only a few saccades and some subjects fixated on only one or a few of the dots. In comparison, when drawing while viewing a displayed cartoon face, subjects made systematic eye movements, closely coupled to the execution of the drawing itself, as also seen in the laboratory and discussed in the companion paper (Tchalenko and Miall 2007).

Drawing – general observations

Drawing within the scanner was of reasonable quality in most subjects, given the difficulties caused by having to hold a drawing pad across the lap, to draw without vision of the hand or the

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paper, and with restricted lateral elbow motion because of the scanner bore. The main effect of these constraints was that drawings tended to be small, typically about 5-8 cm in extent (Figure 3, top row), and the spatial location of some drawn parts was inaccurate (e.g. the ear or eye might be misplaced within the outline of the face, Figure 3C).The drawings shown on the top part of Figure 3, performed during successful eye-tracking, were some of the better drawings produced in the scanner. As expected, drawing from memory (Figure 3A) was noticeably less accurate than when drawing the displayed face in either the combined drawing condition or the new drawing condition (Figure 3C). However in almost all cases, the drawings were recognisable, and key features of each cartoon were normally identifiable, for example the hairline, nose or chin, which were often the most characteristic features (Figure 1). Curiously the two drawings from memory shown in Figure 3A (drawn by different participants, one in the scanner and one in the laboratory) have the same mistake, as the hair quiff has been reversed; the eyebrow is also missing from the upper drawing.

FIGURE 3 NEAR HERE

Functional activations

Analysis of the functional activation patterns used the high level task of mental arithmetic as the baseline condition. Hence we expected to find some conditions evoked lesser activity than the baseline, and indeed this was the case. However, our key results are made from comparisons between conditions, for example between encoding faces versus dots, and the negative activity relative to baseline is irrelevant in such comparisons.

1. Encoding faces

Contrasting the condition in which subjects viewed a new face and encoded it into memory for subsequent drawing (EV2) versus exploration of a field of random dots (EV3) lead to strong activation of extrastriate areas, including the bilateral lateral occipital cortex (Figure 4A) and fusiform face area (FFA, (Grill-Spector et al. 2004c)). There was also significant activation of right

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superior parietal lobe (BA7), left inferior parietal cortex (BA 40), and bilateral ventral and dorsal premotor cortex including the frontal eye fields (Table 1). The activation pattern across all test conditions in the left face-sensitive region of the lateral occipital cortex (LO-faces) is shown in Figure 4C. While identified by the significant difference between the EncodeFaces and ExploreDots conditions, this area was active in all three conditions when the cartoon face was displayed on screen, i.e. EV2, 7 and 8. Very similar activation data was found for right LO-faces. Figure 4B,D shows the activation pattern in right premotor cortex (Cluster 2, Table 2), again showing high relative activity (less negative % signal) for all three conditions with the displayed face. The left superior parietal cortex, BA7, also demonstrated the same strong difference between the two encoding conditions (EV2 versus EV3; see Figure 6D) but also showed high activity during all three drawing conditions when active control of the right drawing hand was needed. Activation of the right FFA appears to overlap the anterior lobe of the cerebellum, and whether there is a clear secondary activation within the cerebellum was not certain for this comparison.

FIGURE 4 NEAR HERE

TABLE 1 NEAR HERE

2. Retention of faces

No significant differences were found for the retention interval, comparing the interval that followed encoding of faces versus the interval that followed exploration of random dots (EV4 – EV5). However, the activity in the lateral occipital cortex seen in encoding faces, while greatly reduced during retention (Figure 4C), was actually significantly lower than during retention of the random dots. Hence there is no evidence of any residual activation of LO or of FFA contributing to the memory of the face to be drawn.

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3. Drawing

The three active drawing conditions (drawing from memory, drawing without memory, and combined drawing with both memory and vision) showed grossly similar overall patterns of activation, including the left sensory motor cortical areas, supplementary motor area, premotor and parietal areas, and activation of right anterior and posterior lobes of the cerebellum. Thus the drawing task activated most of the dorsal stream areas considered to control and guide the hand, as well as frontal areas concerned with planning the sequence of hand actions. For the two drawing conditions in which there was a cartoon face on screen, CombinedDraw and NewDraw, there was no significant activation of the early visual areas, but strong activation was seen of the extrastriate areas including MT/MST and the lateral occipital face area (eg Figure 4C). The lack of significant additional activity in the primary visual cortex in these contrasts compared to baseline is thought to be because of the high levels of visual processing within the baseline mental arithmetic condition in which subjects were viewing the displayed numbers that were to be subtracted.

3.1 Drawing from memory

Comparison of the drawing from memory condition (EV6) versus drawing a face seen for the first time (EV8) identified activation differences due to drawing from memory. Any processes common to both tasks, such as execution and guidance of the hand movements, would not be seen in this contrast. Activity was found in dorsal and ventral prefrontal cortex, in the anterior cingulate cortex, and in the left inferior parietal cortex (Table 2).

FIGURE 5 NEAR HERE

TABLE 2 NEAR HERE

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In order to identify areas involved in encoding and recall of the memory of the cartoon faces, in other words areas showing increased activation both during encoding of the faces (without active drawing) and during the subsequent recall of these encoded memories (during the active drawing stage, without on-screen display of the cartoon) we performed a conjunction analysis. This was the conjunction (Figure 6, yellow clusters) of the positive activation difference for encoding of faces versus dots (EV2-EV3; Figure 4) with the positive activation difference for drawing from memory versus drawing new (EV6-EV8; Figure 5) and identified common activation only in the left inferior parietal cortex (BA 40) and premotor cortex (BA44).

FIGURE 6 NEAR HERE

3.2 Drawing from vision

Comparison of the condition of drawing a face seen for the first time (EV8) versus drawing from memory (EV6) identified activation differences due to active use of vision to guide the concurrent production of the unseen drawing on paper. As before, processes common to both drawing tasks, such as execution of the hand movements, would not be contribute to this contrast. There was, as expected, strong activation of bilateral visual areas including the fusiform face area, bilateral posterior parietal cortex and the frontal eye fields (Figure 7, Table 3). The latter may reflect uneven ocular-motor activity in the drawing from vision condition compared to drawing from memory. There was also very noticeable bilateral activation in the fusiform cortex (FFA) overlapping with a cluster in the anterior lobe of the cerebellum (as identified by an apparent second local maximum with the cerebellar volume, lobule VI) and a separate cluster within the posterior vermis, lobule VIII. There was also activation of the precuneus.

FIGURE 7 NEAR HERE

TABLE 3 NEAR HERE

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To identify areas showing significant increased “on-line” processing of faces, in other words with activation both during viewing of faces during the encoding phase and during the subsequent drawing of the faces from the on-screen display, we performed a second conjunction analysis. This was the conjunction (Figure 6, blue clusters) of the positive activation difference for drawing new versus drawing from memory (EV8-EV6, Figure 7) with the positive activation for encoding of faces versus dots (EV2-EV3, Figure 4), and identified common activation in bilateral lateral occipital cortex (the LO-faces area), in the fusiform face area (FFA) and in superior parietal cortex (BA 7). As before, the cluster in the FFA appears to overlap with a cluster in the anterior lobe of the cerebellum.

Discussion

We aimed to decompose the process of copying a visual image of a face into several component steps: the encoding of a visual image into short-term memory, the retention of this memory, and the subsequent drawing of the memorized face. We therefore contrasted encoding of cartoon faces versus the visual scanning of a random field of dots, tested for differences in the ensuing retention interval, and contrasted drawing of the memorized images against drawing a newly presented image. The main results that have emerged are, first and as expected, that encoding of the visual image of a cartoon face involves considerable activation of extrastriate visual areas in the lateral occipital cortex as well as in the fusiform face area, consistent with the participants treating the image as a representation of a face. Second, we found no overt face-specific activation of occipital areas during the memory retention interval. This suggests that the visual information is not retained as continued activation within these visual face processing areas, but is instead converted into more refined visuo-motor or spatial signals in order to guide the subsequent drawing actions. Third, our data suggest that the act of drawing “blind” without direct vision of the hand or the paper is still a strongly visually guided action, dependent on visual input,

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with powerful activation of the extrastriate visual cortex, parietal and premotor cortices and of the cerebellum. Finally, we found that there is activation of frontal cortical and anterior cingulate areas during drawing that we suggest contributes to planning and self-monitoring of the on-going drawing process, because the pencil and paper cannot be seen and thus monitoring is needed to correctly position lines on the page and to avoid repetition of component of the drawing that have been completed. In addition by performing a conjunction analysis we identified areas that were active in both encoding and in drawing from memory, which we suggest may be areas concerned with the short-term store and recall of the planned drawing actions. A second conjunction identified areas active in encoding and in drawing without memory, and may be areas concerned with processing the visual image, but not in storage.

To discuss these processes in more detail, we start with the activity during initial encoding, The fusiform face area has been identified on the basis of its selective activation by faces over and above responses to other visual stimuli (such as cars, houses etc; (Grill-Spector et al. 2004b; Kanwisher et al. 1997). In the encoding phase, in which we contrast the activity when visually exploring the cartoon faces each seen for the first time against activity when exploring a randomly positioned set of random dots, we did see preferential activation of the FFA, but the activation was strongest in the lateral occipital cortex, in areas corresponding to the region which is sometimes known as LO-faces (Grill-Spector et al. 2004a). There was also broad activation across much of extrastriate visual cortex, and we suggest this is in part because our task involved active exploration of the display, with on average about 40 fixations across the scene. The effect of eye movement was balanced across the encoding faces and exploring dots conditions, but the motion across the retina of the more complex multiple line stimuli in each cartoon, compared to the dot stimuli, could not be controlled for. Interestingly, we also found significant activation of premotor areas (dorsal and ventral premotor cortex) and in the frontal eye fields. Assuming our control for the number of gaze shifts per second was approximately correct, these increased signals suggest that the process of encoding the face information involved higher motor and oculomotor areas concerned with planning actions of hand and eyes. It may therefore suggest that the facial information is encoded as a motor plan.

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In the retention interval, when participants were fixating a cue on an otherwise empty screen, and were retaining the facial information for subsequent drawing, we had hypothesised that the short-term memory trace might be seen as retained signal within the face-processing areas, in analogy to the activation in visual cortical areas when performing visual imagery (Chen et al. 1998a; Ganis et al. 2004a; Ishai et al. 2002b; O'Craven and Kanwisher 2000a). However, this was not found, and in fact the activation in the lateral occipital regions was depressed relative to the activation after the random dots (Figure 4C, EV4 vs 5). No significant retention activation was seen elsewhere in the brain. This negative result may reflect insufficient statistical power, with subtle activation at some locations in the visual brain being present but not strong enough to be identified as significant cluster activity. However, our scan protocol included 36 minutes of functional imaging per subject on a modern 3T scanner. In comparable experimental periods we have been able to detect very strong task related signals. Hence while lack of evidence of a BOLD signal is not evidence for no signal, we do not believe a positive activation during the retention period has been missed due to lack of statistical power. Having explored the relative signal strengths at all the maxima and at many local maxima within clusters that were identified in the other comparisons between conditions, we have found no evidence for any regions in the occipital cortex being more active in the interval after encoding faces than after encoding dots. Two frontal lobe regions were more active, albeit not identified as statistically significant clusters. These were in the right insula (x=40, y=24, z=-4) and right premotor cortex (x=56, y=34, z=16), again suggesting that the facial information was transformed and stored within motor areas, as planned actions. Thus we suggest the facial information is captured through a series of gaze fixations that locate features of the cartoon that are important for its subsequent rendering as a drawing. The gaze pattern during encoding of a cartoon face, under instructions that it must be later drawn, is quite different from the pattern of gaze fixations seen if participants are instructed to identify the face (Tchalenko and Miall 2007). It implies that shifting the gaze during the encoding processes stores the face as spatial locations for subsequent eye and hand actions. If correct, then we might not see any visual cortical activity associated with the retention of the “mental image”, as the image is already transformed into a plan of actions.

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The suggestion of no pronounced occipital activity associated with the retention of faces was then reinforced by the comparison between drawing from memory, without an on-screen displayed face, versus the drawing of a newly seen face, without memory. Here significant activation was largely in frontal, premotor and parietal areas (Figure 5; Table 2). The activation in left inferior parietal cortex (BA 40) was highest when drawing from memory or when writing and page turning (Figure 5E), and was also higher when encoding faces than encoding dots. We suggest that these parietal and premotor areas are activated because the encoding process converts the spatial information gained while viewing the faces into a series of intended motor actions or as spatial targets for motor actions; we cannot separate these alternatives in this experiment. This interpretation is in line with the general theme of vision for action (Goodale and Milner 1992) and would invoke activity in dorsal stream areas of the brain. It is therefore interesting that the conjunction between activity seen in encoding and activity seen when drawing from memory, as shown in the yellow areas in Figure 6, was restricted to two regions, in premotor and parietal cortex. Both are involved in visually guided actions (Battaglia-Mayer et al. 2003; Caminiti et al. 1999). Another area strongly activated during drawing from memory was the anterior cingulate (Figure 5D). This region was activated relatively highly during the retention interval and during drawing from memory, and was not active when drawing from displayed faces (EV7, EV8). We suggest this area may therefore be involved in planning and monitoring the drawing actions (Rushworth et al. 2007), in part to ensure that the sequence of lines drawn from memory is not repeated or skipped over.

Drawing from visually displayed cartoon faces, not surprisingly, powerfully activated occipital visual areas, as the visual face information would be needed to guide the unseen drawing action of the hand. Interestingly, the activation in LO was greater in the new drawing condition than in the initial encoding stage (Figure 4C, EV8 vs EV2), suggesting that the need for active use of the visual face information, as well as potentially enhanced attention to vision, drives this area strongly. We also saw activation of cerebellar vermis (Figure 7B), superior parietal cortex, and premotor and supplementary motor areas, areas that would be necessary to control the hand actions. One interpretation of this motor activity is that it reflects the use of efference copy signals

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of the hand (and/or) eye movements during the drawing action. This efference copy signal would be expected to help predict the outcome of the actions (Miall et al. 1993), and Land (Land 2006) has suggested that visual input might be stored in a buffer to help control the subsequent actions (Wilmut et al. 2006). This implies that visual inputs are available for a short period after each eye gaze, and this indicates that even though the hand is not seen, it is functionally guided by visual information. The same process is very likely to guide hand actions in other tasks, for example when we visually locate an object to be grasped, or a target on which to place a held object, but then turn our gaze away before the grasping or placing action is performed. Thus "visual guidance" might be thought to be a process that uses visually gathered information to guide hand action, even in the absence of direct visual control of the action, probably through a visuo-motor transformation in which the visual data defines the desired hand path (Flanders et al. 2006b; Miall et al. 2001; Miall and Reckess 2002; Reina and Schwartz 2003; Sergio and Scott 1998). There is also a growing literature that suggests that apparently uninformative visual input, which may even be limited to gazing at an obstructing panel blocking view of the hand, can improve manual performance (Newport et al. 2002), and this implies that the gaze position is used to help control manual actions, with or without concomitant visual information reaching the retina.

In the conjunction of drawing without memory with the activity when encoding faces, we found common activation of the face sensitive areas in lateral occipital and fusiform cortex and in the superior parietal cortex (blue clusters, Figure 6). Again this suggests that the encoding process may be converting the displayed face into a series of spatial loci or as a series of planned actions (Andersen et al. 1997; Buneo and Andersen 2006). When drawing new, each identified line on the cartoon is captured and drawn in turn; when encoding for subsequent drawing, the same process may take place, but the intended action is delayed until the later drawing phase (Andersen and Buneo 2002). In the companion paper (Tchalenko and Miall 2007), we show that the gaze paths during encoding and drawing are often strikingly similar and hence seem to follow along the same sequence of chosen landmarks. However, when drawing from memory in the scanner, we displayed a random field of dots in order to attempt to balance the visual input. One consequence of this was that the participants' eyes were often fixated on one or more dots for

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long periods during the drawing phase (Figure 3B top). In contrast, in the laboratory conditions in which a blank sheet obstructed view of the hand, preliminary analyses indicate that the eyes sometimes moved in sequence to locations that approximately matched the drawn lines. Thus in some but not all participants the gaze movements offered a window onto the unfolding plan of the drawing from memory. Further work will be needed to explore this both in the laboratory and in the scanner.

Like any imaging study, there are compromises that must be made in taking a behavioural task into the functional imaging environment. First, to reduce the overall duration, we decided to make the mental arithmetic and page turning conditions shorter than the others. This may have the effect of weakening the statistical comparisons (Birn and Bandettini 2005), but in a complex design such as this one, where the baseline is contrasted with several other EVs, it is not clear what effect, if any, such relative changes in block duration would have. Moreover, the comparisons of most importance were between conditions of equal length, controlling only the factor of face or dot processing. Next, choice of a baseline condition is always problematic (Gusnard et al. 2001; Shulman et al. 2007). Most of the activations we report are less than the baseline. However, a simple, empty, rest condition would have allowed subjects to remember the faces from the preceding trial and given the strong task relevance of face processing we felt it quite likely that they would, given the chance during rest, actively recall these images. Hence we decided to use a demanding, visually based task that would conflict with visual face processing and would require working memory resources, in order to “wipe the slate clean” of any face processing. The fact that this is a demanding condition is irrelevant to the analysis, as it simply means the “baseline” is high, and hence the signal in some of the blocks of interest is negative with respect to this arbitrary level. As above, the most interesting results come from comparisons of encoding faces and dots, so the absolute level of signal is not considered. There could also be order effects which are unavoidable, as the encoding must always precede the retention stage, etc. Any temporal overlap from the PageTurn to the immediately following Encode condition, or between other condition pairs, is not a serious issue as we are only concerned with the relative differences in activation between, for example, encoding faces and encoding dots. They both

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have a common time relation to the preceding Turn Page condition, and so any functional overlap from TurnPage to Encode would be common to both. Finally, the Retention period, in which we saw very little signal might be though of as a null condition, in which subjects were not on-task. However, they were explicitly instructed to remember the faces, and hence we hypothesised differential working memory during the retention of faces and the "retention" of the explored dots. Moreover, they did not know which trial type they were in; the presentation of faces in the encode stage could be followed by either the same face again (CombinedDraw) or by the dots (DrawMemory). Hence they had to memorise the face in both conditions. In the DrawNew condition the dots did cue them about the subsequent drawing condition, but they would not know what face they would subsequently see, as a new cartoon face was used in every trial.

In summary, we have shown that the process of viewing a simple cartoon of a face, with the intention to subsequently reproduce the drawing, has a number of key elements. First, the facial information is captured through a task-specific pattern of gaze fixations on features of the cartoon, different from those made to identify the face (Tchalenko and Miall 2007) and, we suggest, this implies that shifting the gaze stores the face as spatial locations for subsequent eye and hand actions. Second, we could not identify visual areas concerned with retention of the signals, although there is a further hint that the premotor cortex is a possible site of retention as a motor plan. Subsequently, the drawing process recreates these planned actions as the eye and hand are guided by the retained visuo-motor information and the drawing proceeds under executive control from higher frontal areas. Finally we see this work as evidence that we can use functional imaging, in combination with eye and hand tracking, to decompose apparently complex visuo-motor tasks into functional stages. We are now in a position to combine simultaneous functional imaging with eye-tracking and 3-D tracking of the hand; more work will follow.

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Figure 1: a selection from the 48 cartoons used in the study.

Figure 2: Task sequences. Each trial type (columns A-C) consisted of 5 blocks (rows i-v). The baseline Subtract condition (i) and TurnPage conditions (ii) were common across all trials albeit with different numbers on every trial. In the NewDraw trials (A) they were followed by an ExploreDots block (A,iii); hence the subsequent RetainDots block (A,iv) had no face memory component and was followed by the NewDraw condition (A,v) in which a new cartoon was displayed for immediate drawing. In the CombinedDraw trials (B), the same cartoon face was shown before (B,iii) and after (B,v) the retention condition, with a new cartoon on each trial. In the MemoryDraw trials (C) the cartoon was shown only once (C,iii) and the subsequent drawing performed from memory while only random dots were displayed on screen (C,v). The correspondence between conditions and the 8 explanatory variables used in the GLM model of the data is indicated by the labels EV1-8; the Subtract condition was the unmodelled baseline.

Figure 3: Comparison of eye gaze patterns and drawings produced by two different subjects, one in the scanner (top row) and one in the laboratory (bottom row). The left columns in panels A and C show the cartoon images and the eye scan paths; the right columns show the produced drawings. Panel A was for the drawing from memory condition, in which the cartoon was viewed and then removed from vision. The drawings in the scanner (panel A, top) were produced while viewing a random field of dots; the drawing in the laboratory were with a blank easel. Eye scan-paths during the drawing-from-memory phase shown in panel A are shown in panel B. Panel C shows cartoon faces draw without memory (while the cartoon was viewed for the first time, or “direct blind copying” as described in (Tchalenko and Miall 2007). The sizes of the circles on the scan-paths in all three panels indicate the duration of each fixation; durations were greatest when fixating the random dots.

Figure 4 Encoding faces: Panels A, C: functional activation identified by contrast of encoding of cartoon faces versus exploration of a field of randomly positioned dots. **A:** The cross-hairs are located in the face sensitive area of the lateral occipital (LO-faces) at x=-42, y=-86, z=-4 mm. **B:** right premotor cortex, coordinates x=40, y=0,z=42 mm (Table 1). **Panels C,D:** Mean activation levels (+/- 1SE, n=13) across the 8 task conditions (EVs 1-8),

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for local maximum identified by the contrast shown in panels A, B respectively. EV1: TurnPage; EV2: EncodeFace; EV3: ExploreDots; EV4: RetainFace; EV5: RetainDots; EV6: MemoryDraw; EV7 CombinedDraw; EV8: NewDraw. The contrasts in panel A and B corresponds to the difference between the grey bars, EV2-EV3.

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Figure 5 Drawing from memory versus drawing without memory. Functional activation identified by contrast of drawing of cartoon faces from memory (MemoryDraw) versus drawing new faces with on-screen display (NewDraw). The cross-hairs are located at **A:** x=-40, y=-48, z=32 mm; **B:** x=40, y=24, z=-4 mm; **C:** x=-46, y=6, z=18 mm; **D:** x=-4, y=34, z=26 mm (Table 2). **Panels E and F:** Mean percentage signal change (+/- 1SE, n=13) for local maxima shown in panels A and D; the contrast in panel A corresponds to EV6-EV8; see Figure 4 for details of each EV. **E:** left inferior parietal cortex, ar coordinates shown in panel A; **F:** Anterior cingulate, at coordinates shown in panel D.

Figure 6 Conjunction of encoding faces and drawing. Functional activation identified by conjunction between the activation seen during of drawing of cartoon faces from memory versus drawing new faces with on-screen display (EV6 – EV8; Figure 5) and the activation seen during encoding of faces versus exploration of dots (EV2 – EV3; Figure 4) is shown in **yellow**. Clusters are located in the premotor cortex, BA44 (**A:** x=-48, y=12, z=22 mm) and the inferior parietal cortex, BA 40 (**B top:** x=-38, y=-52, z=42 mm).

The opposite conjunction between the activation seen during of drawing new faces with on-screen display versus drawing of cartoon faces from memory (EV8 – EV6; Figure 7) and the activation seen during encoding of faces (EV2 – EV3; Figure 4) is shown in **blue**. Bilateral clusters are located in the faces sensitive LO-area, extrastriate cortex, BA 19 (**A bottom)**, superior parietal cortex, BA 7 (**B top**) and in the fusiform face area, BA 37 (**B:** x=+/-40, y=-50, z=-20 mm).

Figure 7 Drawing new versus drawing from memory. Functional activation identified by contrast of drawing of new faces with on-screen display (NewDraw) versus drawing cartoon faces from memory (MemoryDraw). The cross-hairs are located at **A:** x=-40, y=-48, z=32 mm; **B:** x=-20, y=62, z=56 mm (Table 3). **Panels C and D:** Mean percentage signal change (+/- 1SE, n=13) for local maxima identified in this contrast, corresponding to EV8-EV6; see Figure 4 for details of each EV. **C:** left SMA, BA 6, at coordinates x=-4, y=-22, z=54 mm (Table 3). **D:** Left superior parietal cortex, at coordinates shown in panel B (see also Table 3).

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Cluster Vol cc	Cluster P	Z-MAX	X (mm)	Y (mm)	Z (mm)	BA	Anatomical locus
236.7	<0.00001	5.82	-42	-86	-4	19	Lateral Occipital L
		5.37	-44	-50	-24		FFA/Cerebellum Lobule VI L
		5.32	36	-86	-10	19	Lateral Occipital R
6.3	0.0004	4.04	40	0	42	6	Premotor cortex R
		3.73	30	6	44	6	Dorsal Premotor cortex R
		3.61	30	2	56	8	Frontal Eye Field R
		3.44	44	-2	38	6	Ventral Premotor cortex R
5.8	0.0008	4.51	54	-30	52	2	Somatosensory cortex R
		3.50	56	-24	40	3	Somatosensory cortex R
		3.49	62	-24	38	1	Somatosensory cortex R

Table 1: Comparison of functional activation during encoding of faces versus the exploration of a series of randomly positioned dots. Three clusters identified based on a z-score threshold of z=2.3 and a corrected cluster probability of p=0.05 are reported by volume and cluster-level probability. Local maxima within each cluster are identified by coordinates in the MNI-space, Broadman's area number, and anatomical locus.

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Cluster Vol cc	Cluster P	Z-MAX	X (mm)	Y (mm)	Z (mm)	BA	Anatomical locus
21.4	<0.00001	3.94	-46	6	18	6	Ventral premotor L
		3.90	-38	16	26	48	Frontal Inf Tri Ventral premotor L
		3.66	-54	10	2	48	Ventral premotor L
19.0	<0.00001	4.07	-4	34	26	32	Ant cingulate L
		4.03	0	30	36	24	Frontal Sup Medial
		3.93	-2	14	52	6	Supp Motor Area L
		3.88	-2	26	30	24	Cingulum Mid L
5.1	0.0036	3.60	40	24	-4	47	Frontal Inf Orb R Insula
		3.28	52	14	12	44	Frontal Inf Oper_R
4.7	0.0064	3.44	-40	-48	32	40	Parietal Inf L
		3.21	-36	-56	40	40	Angular L
		3.19	-64	-38	38	40	SupraMarginal L

Table 2: Comparison of functional activation during drawing faces from memory, without simultaneous display of the face versus drawing without memory, from a previously unseen simultaneous display. Clusters identified based on a z-score threshold of z=2.3 and a corrected cluster probability of p=0.05 are reported by volume and cluster-level probability. Local maxima within each cluster are identified by coordinates in the MNI-space, Broadman's area number, and anatomical locus.

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Cluster Vol cc	Cluster P	Z-MAX	X (mm)	Y (mm)	Z (mm)	BA	Anatomical locus
274.4	<0.00001	6.22	-44	-86	-4	19	Occipital Inf L
		6.00	-30	-66	-20	-	FFA/Cerebellum Lobe VI L
		5.92	26	-88	-12	18	Occipital Inf R
		5.75	44	-60	-22	37	Fusiform R
		5.72	46	-82	-6	19	Occipital Inf R
19.0	<0.00001	4.09	0	52	-20	11	Rectus
		3.98	14	68	12	10	Frontal Sup R
		3.95	4	70	2	10	Frontal Sup Medial R
		3.93	-6	60	24	10	Frontal Sup Medial L
		3.85	-2	48	-14	11	Frontal Mid Orb L
		3.85	-16	58	30	9	Frontal Sup L
14.4	<0.00001	4.16	-20	-62	56	7	Parietal Sup L
		3.70	-38	-12	48	6	Precentral L
6.4	0.0006	3.65	-4	-22	54	6	Supp Motor Area L
		3.38	-10	-26	46	?	Cingulum Mid L
6.1	0.0011	3.32	56	-6	-20	21	Temporal Mid R

Table 3: Comparison of functional activation during drawing new, from a previously unseen displayed cartoon, versus drawing faces from memory without simultaneous display. Clusters identified based on a z-score threshold of z=2.3 and a corrected cluster

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probability of p=0.05 are reported by volume and cluster-level probability. Local maxima within each cluster are identified by coordinates in the MNI-space, Broman's area number, and anatomical locus.

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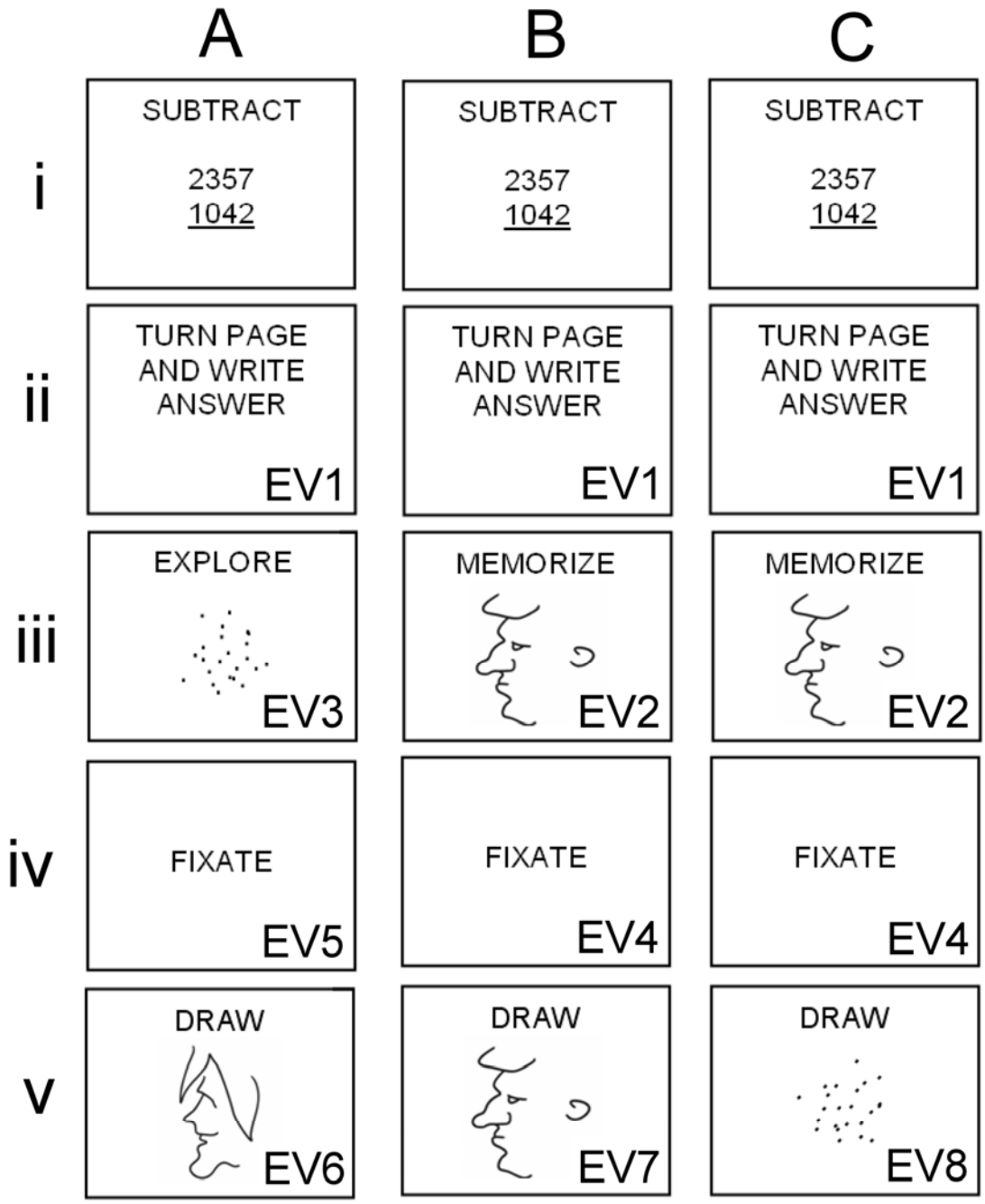
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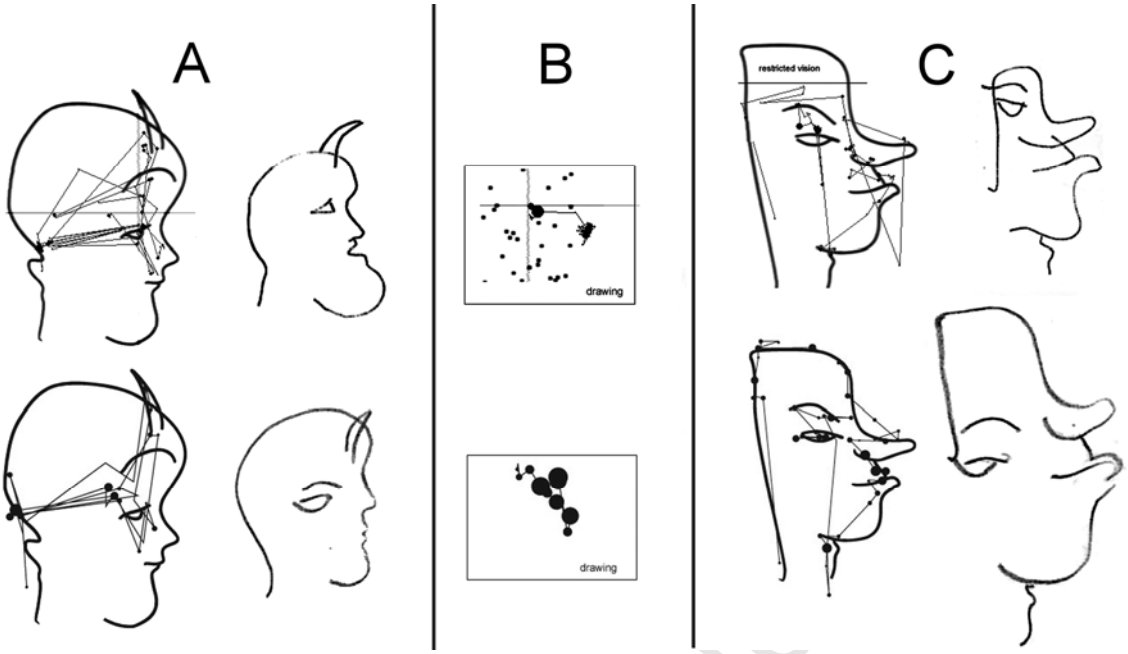
DRAW
EV8



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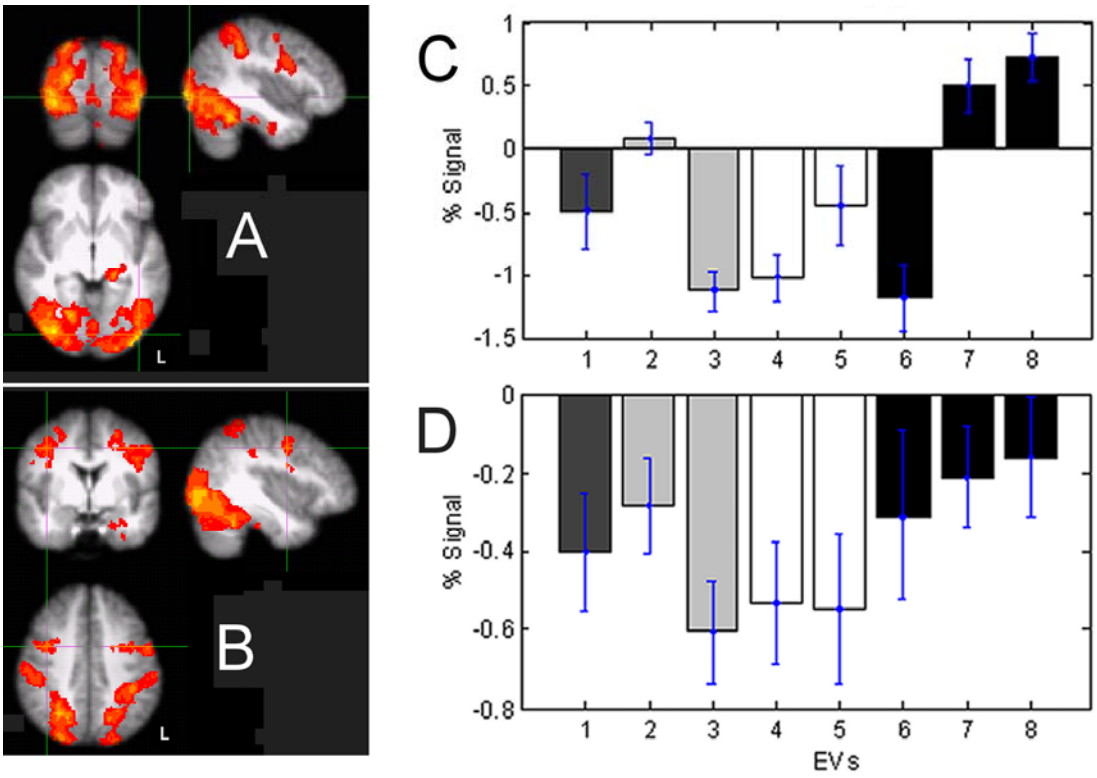
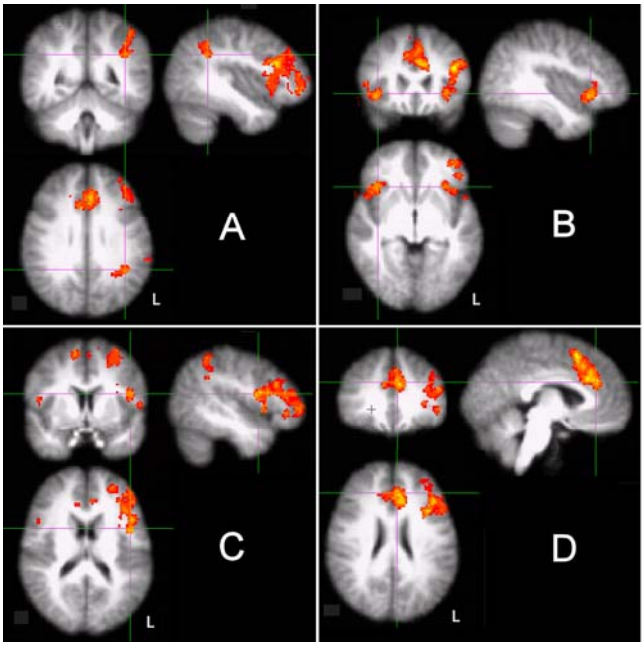
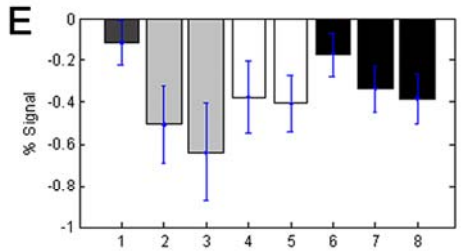
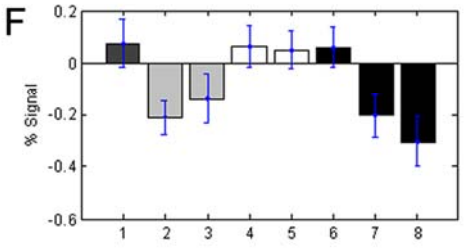

A
L
B
L
C
% Signal
1
0.5
0
-0.5
-1
-1.5
1 2 3 4 5 6 7 8
D
% Signal
0
-0.2
-0.4
-0.6
-0.8
1 2 3 4 5 6 7 8
EVs

ACCEPTED M







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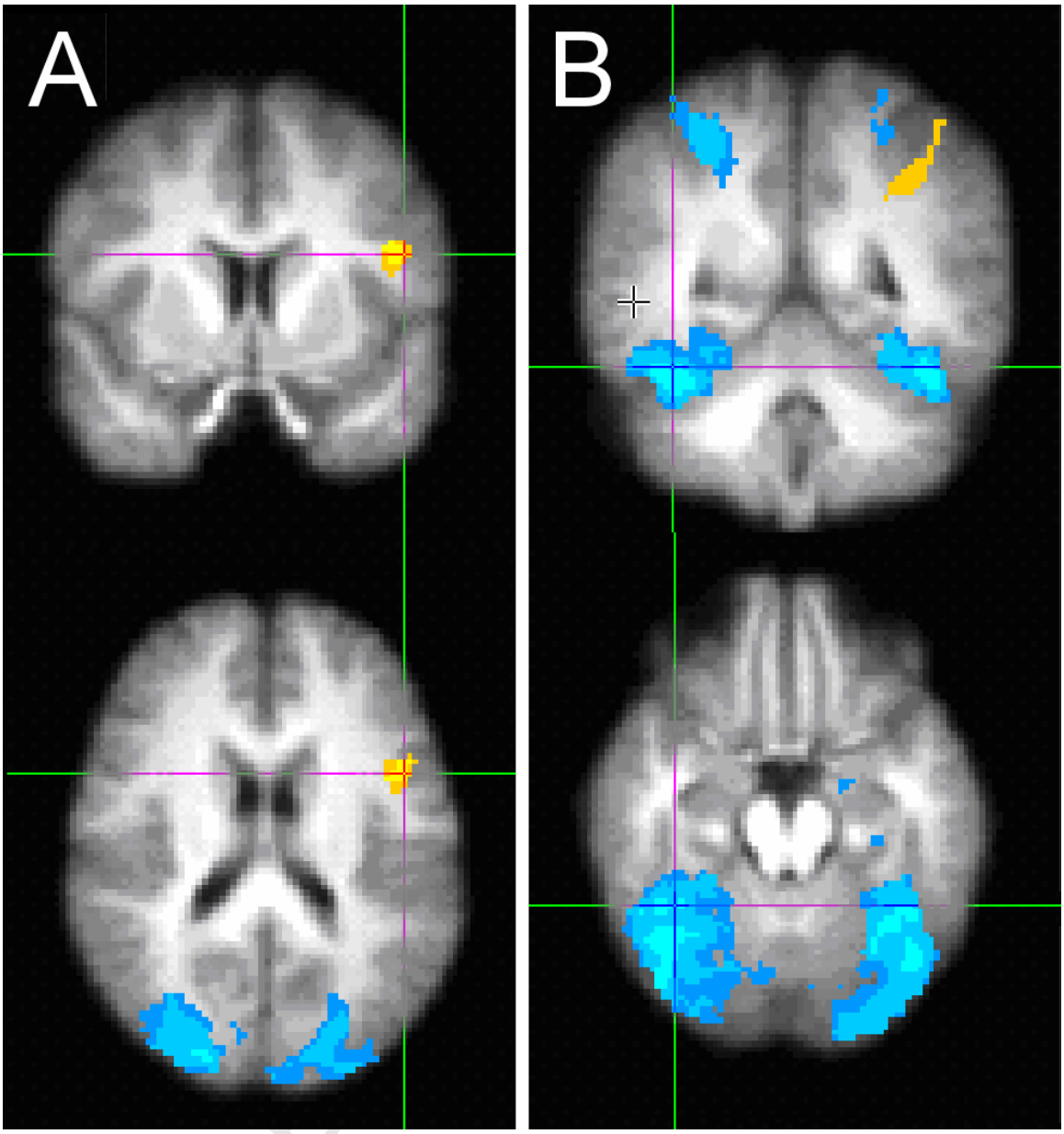

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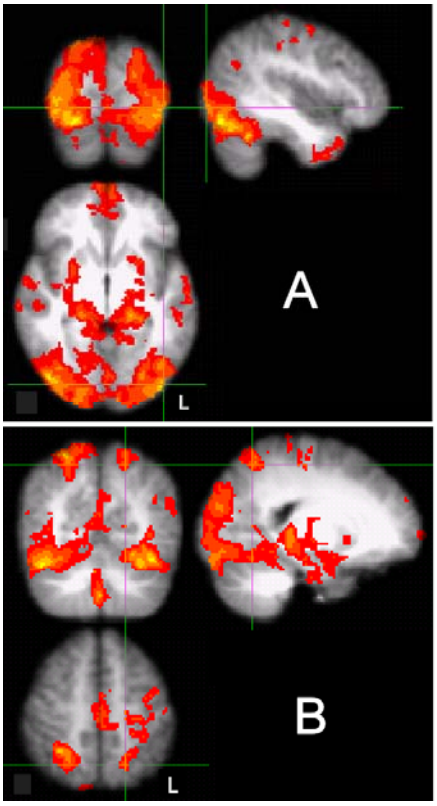
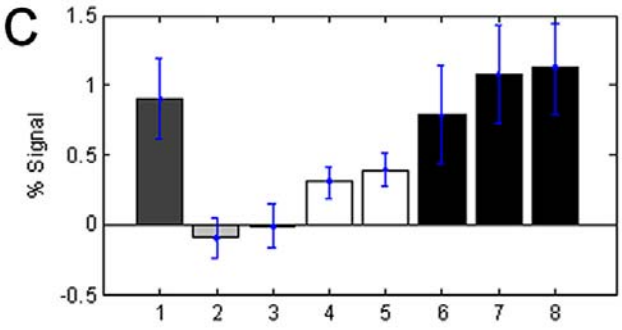
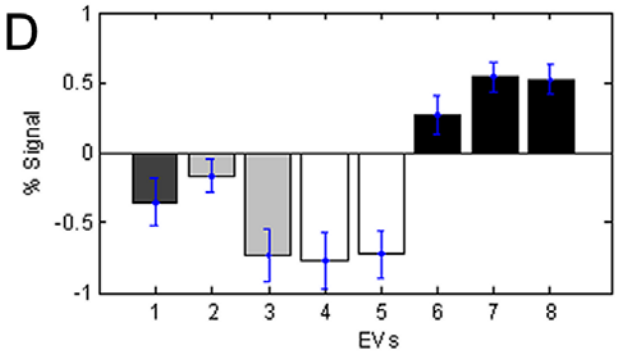

A
L
B
L


C
% Signal
1.5
1
0.5
0
-0.5
1
2
3
4
5
6
7
8


D
% Signal
1
0.5
0
-0.5
-1
1
2
3
4
5
6
7
8
EVs

ACCEPTED M