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Research report

fMRI-activation during drawing a naturalistic or sketchy portrait

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HIGHLIGHTS

- ► We used fMRI to measure 20 naive subjects during drawing a portrait.
- ► Participants were able to track their drawing online.
- ► We identified three important circuits specific for the process of portrait drawing.
- ► Circuits where: face perception, location encoding, and continuous feedback processes.
- ► Representations involved: fusiform gyrus, precuneus, parietal sulcus, and cerebellum.

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ABSTRACT

Neural processes for naturalistic drawing might be discerned into object recognition and analysis, attention processes guiding eye hand interaction, encoding of visual features in an allocentric reference frame, a transfer into the motor command and precise motor guidance with tight sensorimotor feedback. Cerebral representations in a real life paradigm during naturalistic drawing have sparsely been investigated. Using a functional Magnetic Resonance Imaging (fMRI) paradigm we measured 20 naive subjects during drawing a portrait from a frontal face presented as a photograph. Participants were asked to draw the portrait in either a naturalistic or a sketchy characteristic way. Tracing the contours of the face with a pencil or passive viewing of the face served as control conditions. Compared to passive viewing, naturalistic and sketchy drawing recruited predominantly the dorsal visual pathway, somatosensory and motor areas and bilateral BA 44. The right occipital lobe, middle temporal (MT) and the fusiform face area were increasingly active during drawing compared to passive viewing as well. Compared to tracing with a pencil, both drawing tasks increasingly involved the bilateral precuneus together with the cuneus and right inferior temporal lobe. Overall, our study identified cerebral areas characteristic for previously proposed aspects of drawing: face perception and analysis (fusiform gyrus and higher visual areas), encoding and retrieval of locations in an allocentric reference frame (precuneus), and continuous feedback processes during motor output (parietal sulcus, cerebellar hemisphere).

1. Introduction

1.1. General issues

Drawing naturalistically is a capacity unique to humans [1]. Trained chimpanzees are at most able to develop a simple form of structured drawing guided by a visual model [2]. Even more specialized is the human capacity to draw sketches, which emphasize characteristic properties of a face. When drawing from life, the three-dimensional scene of the external world is transformed into a sequence of hand movements that produce a two-dimensional picture on the paper. When producing a line drawing portrait from a photograph of a face, the transfer is not from three-dimensional to two-dimensional, but from a picture coding brightness continuously into a graph showing mainly contours of areas with similar brightness.

With respect to neural processes involved, drawing an object is a complex visuo-motor task. Arm and hand are moved to reproduce a spatial arrangement of visual elements by applying motor routines in a tight sensorimotor interaction [3,4]. This sensorimotor interaction is especially centered on visual but also some somatosensory feedback. Visual feedback includes the developing drawing as well as the location and movements of the hand and pencil.

Copying a figure by drawing as opposed to tracing a figure is a common test of configurational apraxia because copying requires drawing visual elements in correct spatial relations to previously

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drawn parts. Such reproduction of allocentric spatial relations is not required in tracing, which involves target-centered movements only [5]. In the present fMRI study, we contrasted copying and tracing as it was done in previous studies [5–7], however, we examined a particularly difficult drawing task (copying real faces) and retained the task characteristics of visuo-motor coordination and somatosensory feedback. Participants could see their drawing movements and a pencil was used to draw on paper.

Copying an original differs from drawing from memory [3]. When the original to be drawn is available, the eyes alternate between the original and the drawing to minimize memory demands [4]. In many previous fMRI studies of drawing, the developing drawing and the drawing hand were invisible and thus, drawing proceeded without the typical alternating gaze pattern, without visual feedback, and without visual guidance for reaching and hand movements. Participants were asked to draw with a finger in the air that they could not see [8], to draw blindly [3], or to imagine drawing [9]. In some studies at least a cursor and the developing drawing were visible [6,7].

In a study by Gowen and Miall [3] and in the present study, participants drew with a pencil and visual feedback was provided in the scanner through a mirror. Thus, the drawing hand was visible, but eye-hand coordination during drawing had to be adapted similar to, for example, drawing with a mouse on a computer screen. Gowen and Miall's [10] participants were asked to draw simple and familiar shapes from memory. In contrast, in the present study, participants drew portraits with a characteristic alternation of gaze between the original photo of a face and the drawn portrait [4].

Copying a portrait foremost involves face perception. Core areas for face recognition [11] are the occipital face area (OFA) [12], the posterior superior temporal sulcus (pSTS) [13], and the fusiform face area (FFA) [14] in both hemispheres but lateralized to the right side [15]. The pSTS is especially important for evaluating socially relevant aspects of a face such as gaze [16] and monkeys with lesions in the posterior STS suffer from selective gaze recognition but are unimpaired in face recognition [17] - therefore, this structure might not be of high relevance when drawing a naturalistic portrait. Hence, we expect only involvement of the FFA and OFA as found in a fMRI experiment on copying line drawings of cartoon faces [3].

In copying faces, vision serves two functions. Vision is employed for encoding visual elements and spatial relations in the original, and second, vision as vision for action guides and monitors drawing movements. Scanpaths, measured with eye-movement recordings during drawing, reveal edge-following patterns along image contours [18]. By investigating eye and hand movements in beginner art students it has been shown that during copying of a linear caricature of a profile, the eyes alternate rhythmically between the pencil and the corresponding segment of the original [3,4]. Brain areas involved in the control of eye movements overlap with those controlling covert shifts of visual attention. In particular, the frontal eye fields (FEF) or the caudal superior frontal sulcus (cSFS) [19] support visuomotor control and attentional selection.

Vision for visuo-motor control depends on the dorsal visual pathway and medial parietal cortex [20]. Visually guided egocentric reaching predominantly involves the medial IPS [21]. Furthermore, the precuneus seems to support the planning of visually guided reaching and pointing movements [22–24]. Movements not directed towards a visual target but relative to a visual target (allocentric as required in drawing) involve the left intraparietal sulcus (fundus and posterior part), the right posterior parietal lobe (PPL) and the dorsal premotor cortex (dPMC) [5].

In addition to visually guided reaching, drawing requires the skilled handling of the drawing tool by applying motor engrams. Motor engrams are representations of complex motor patterns, which can be activated by execution, imagery, and observation of movements, specific to the patterns trained. In humans, this movement pattern representation is located predominantly in the ventral PMC and the inferior frontal gyrus (pars opercularis-BA44 and pars triangularis–BA 45) [25].

The execution of motor patterns is guided by visual, but also by sensorimotor feedback. Precise feedback of motor performance is of special importance in drawing. Drawing only with the fingers but without a pen involves bilateral primary somatosensory activation but also parietal activation in the superior parietal lobe (BA 5, 7), in the supramarginal gyrus (BA 40; which might overlap with S2-activation), and in the anterior cerebellar hemisphere [8]. All these areas are processing somatosensory feedback control.

1.2. Paradigm and hypotheses

In order to differentiate representation sites characteristic for the process of drawing, we applied functional Magnetic Resonance Imaging (fMRI) in twenty drawing-training-naive subjects during naturalistic and sketchy drawing of a face presented by a photograph. These two copying tasks were intended to reveal differences in the neural correlates of these two manners of drawing that are discerned in drawing classes. Sketchy as opposed to naturalistic copying involves more global visual analysis and a higher speed of movement. The two copying tasks were contrasted with a tracing task and with passive viewing.

By contrasting drawing against viewing of the face we expected activations reflecting motor control, visuomotor control, and sensorimotor control. Differences in visual areas and areas associated with shifting gaze and attention should be observed, too, because the developing drawing results in additional visual stimulation and the alternating gaze pattern occurs in the drawing conditions only.

By contrasting drawing against tracing with a pen we expected characteristic activation reflecting visuo-motor control that is not target-directed as in tracing. Tracing contours with a pen required visually guided motor action and the processing of sensorimotor feedback, however, only drawing required the allocentric encoding of visual features as motor plans that had to be transformed to be executed at another location. Furthermore, drawing but not tracing should produce additional visual stimulation by the developing drawing and the alternating gaze pattern.

2. Method

2.1. Subjects

Twenty, female students of different faculties, without history of neurological or psychiatric disease, were recruited by announcements at the University of Greifswald (mean age 22.45 years; SD = 3.07; ranging from 19 to 31). All participants were strongly right handed (M = 95.83, SD = 10.65) as assessed by the Edinburgh Handedness Inventory [26]. A questionnaire of experience in drawing revealed that participants had only attended art lessons in school (M = 9.55 years, SD = 4.17) but had not received any further training in drawing. The study was approved by the Ethics Committee of the Medical Faculty of University of Greifswald.

2.2. Tasks and materials

Participants were instructed before scanning about the tasks which included (1) passive viewing of the face ("explore the presented face passively"), (2) tracing the contour of the face and its elements with a pencil ("follow the contours of the face with the pencil on the tracing paper affixed above the photo"), (3) sketchy and characteristic drawing ("produce a characteristic and sketchy portrait"), (4) exact and naturalistic drawing ("produce a naturalistic drawing of the face as similar as possible to the presented picture"). For illustration of the paradigm see Fig. 1. The control tasks (tracing the contours and passive viewing) were performed once and the drawing tasks were performed twice. Different numbers of scans between conditions were considered in the statistical design calculation of fMRI-effects. The faces to be drawn or traced were six photographs of females and males (neutral faces selected form the Karolinska Directed Emotional Faces data base; Lundqvist, 1998).

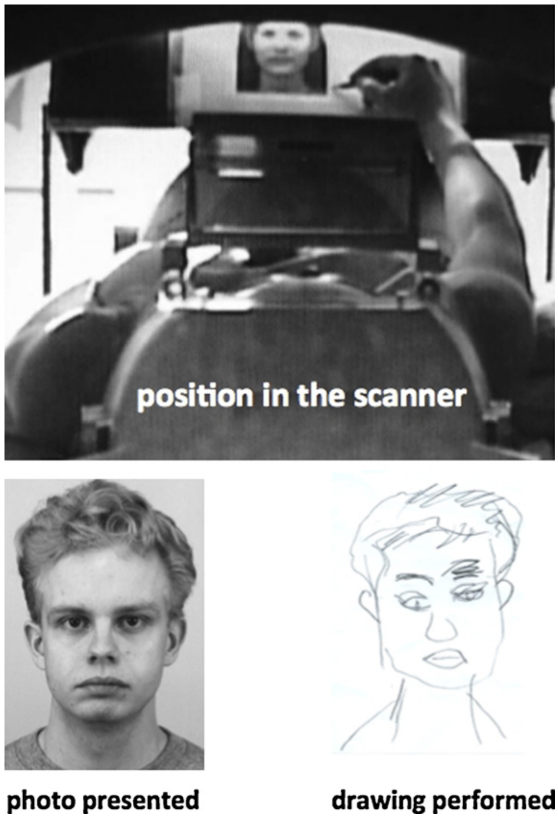

Fig. 1. Illustration of the paradigm: Top: rostral view of the position of the participant in the scanner while drawing. Bottom: left: example of a photo presented; right: example of a sketchy characteristic drawing performed in 90 s in the scanner.

Each face was shown as a 13 by 10 cm print on the left half of a 21 by 30 cm sized sheet of paper. On the right half, space for drawing was provided. The current task was indicated by a headline above the face. The sheets were attached to a scanner desk, which was installed above the subject's chest (see Fig. 1). The paper sheets with photos of the faces and space for drawing were viewed via a double-mirror system attached to the head coil about 10 cm above the eyes. A regular pencil was used for drawing on the paper. The desk position was adjusted to each participant's arm length. The right upper arm was supported by cushions to restrict arm movements during drawing. Moreover, the participant's head was stabilized by foam pads. The participant was instructed to keep the left hand in a relaxed position on the scanner couch. An experimenter standing near to the participant changed sheets and ensured correct performance during scanning. Colored light from a projector indicated activity and resting intervals. The participants were instructed to start with the next task when the light switched from blue to green and to continue until the light switched back to blue. Blue light signaled resting intervals lasting 30 s between tasks.

The passive viewing task, the tracing task, and sketchy drawing lasted 1.5 min each. For naturalistic drawing, 3 min were provided, of which the middle 1.5 min were used for statistical analyses. The conditions were presented in a pseudo-randomized order: the four conditions in random order followed by the second trials of the drawing conditions in random order. The presented faces were pseudo-randomized for the four conditions. Every participant drew four portraits during scanning, two naturalistic and two sketchy.

2.3. Scores and creativity test

Concentration, difficulty of the task and personal success (general drawing quality) during fMRI-tasks were assessed after scanning on a visual analogue scale (VAS; from 0 = "very bad" to 10 = "very good").

The "Test for creative thinking" (TSD-Z; [38]) was performed outside the scanner after fMRI-measurements. This test assesses the figural creative ability by providing irregularly arranged figural elements, starting from which complete figures should be drawn. The drawings were later evaluated based on 14 criteria on scales each ranging from 0 to 6 points. Fifteen participants (75%) completed this test. The drawings produced in the scanner (four per participant) were rated by two experts, both Professors of the Caspar David Friedrich Institute for fine arts of the University of Greifswald. Two items were scored on a 10 cm visual analogue scale: "realistic illustration of the face" for natural drawings and "realization of characteristics of the face" for sketchy drawings.

2.4. fMRI data acquisition

We measured with a 3 T whole body MRI-scanner (Siemens Verio, Erlangen, Germany) using a 32-channel headcoil. Both T1-weighted structural and T2*-weighted echo-planar images (EPIs) used for functional mapping were acquired. EPIs consisted of 320 whole brain volumes (TE 30 ms, TR 2 s, matrix size 64 × 64, flip angle 90°, 33 transversal slices with 3 mm thickness and 1 mm interslice gap). In addition, a T1-weighted anatomical image was acquired with the MPR sequence (TR 2.3 s, TE 3.93 ms, 160 axial slices 1 mm isovolumetric, flip angle 90°).

2.5. fMRI data evaluation

Data were analyzed with statistical parametric mapping software (SPM5, Wellcome Department of Imaging Neuroscience, London) running on Matlab version 7.4.0. (MathWorks, Inc., Natick, MA). We used the default-settings if not indicated otherwise. Unwarping of geometrically distorted EPIs was performed in the phase encoding direction using the FieldMap Toolbox available for SPM5. Realignment was used to correct for movement artifacts. Each time-series were realigned to the first image of each session and resliced. EPIs were coregistered to the T1-weighted anatomical image and T1-weighted images were segmented, which was the basis for spatial normalization in the Montreal Neurological Institute (MNI) space. Smoothing was performed with a 9 mm × 9 mm × 9 mm (full-width at half maximum (FWHM) Gaussian Kernel filter to increase the signal-to-noise-ratio. Movement parameters estimated during the realignment procedure were introduced as covariates of no-interest into the general linear model. For calculation of a first level statistic, the realignment parameters were used as additive regressors for each subject. A temporal high-pass filter (128 s) was applied to remove slow signal drifts. Individual statistical maps (fixed effect) of main effects (*naturalistic drawing, sketchy characteristic drawing*) and the control conditions (*passive viewing, tracing contours*) subtracted from the main effects were evaluated for each subject using the general linear model (task conditions vs. baseline conditions). In order to reduce influences of changing the paper on the drawing desk, we did not consider the first and the last scans of each condition for modeling the main effect. Of naturalistic drawing trials, which each lasted 3 min, the middle 90 s were used for the calculation of first level effects. First level contrast images of each subject were used for group statistics calculated as a random effect analysis at the second level. Effects between conditions were calculated with paired *t*-tests (Tables 1 and 2).

Location of significant representation sites was evaluated using the SPM Anatomy Toolbox Version 1.8 [27] and – for areas not yet available in Anatomy – using anatomical masks from Automated Anatomical Labeling (AAL) software [28]. Brain activations were superimposed on the Montreal Neurological Institute render brain and on the T1-weighted Colin's-single-subject brain. For the comparison between conditions, we report brain activations in preselected regions of interest selected from previous studies on functional representation during comparable tasks as introduced in the Introduction. These regions were the primary and secondary motor areas including the frontal eye field, cerebellar hemispheres, somatosensory cortex, occipital lobe, precuneus and cuneus, MT, middle and inferior temporal lobe including fusiform gyrus, superior and inferior parietal lobe, the cingulate gyrus, and Broca's area and its right hemispheric analogue. We plotted results for these areas with an intensity threshold of $p < .001$ and indicated when activations were significant at the $p < .05$ level (family wise error FWE) for the respective ROI in Tables 1 and 2.

3. Results

3.1. Behavior, ratings and testing

Maximal head movements during actual drawing in the scanner were smaller than 2 mm for all subjects. Participants rated both naturalistic ($M = 6.91$, SE = 2.06) and sketchy drawing ($M = 5.31$, SE = 2.21) as moderately difficult. However, it was easy for them to trace the contours ($M = 2.12$, SE = 1.92), suggesting that the difficulty was associated with their ability to draw and not with an uncomfortable position in the scanner. Overall, they were not very satisfied with the quality of their drawings (naturalistic: $M = 2.91$, SE = 1.74; sketchy: $M = 3.93$, SE = 1.89). In the "Test for creative thinking" (TSD), our students rated with average figural creativity scores ($M = 54.86$, SD = 12.51; average age matched reference population given for the test: $M = 60.60$, SD = 18.70; [38]). Four participants showed a performance below average, nine in the area of average, and only two in the area of above average. The drawings produced in the scanner, rated by experts, were rated poorly for the items most relevant for naturalistic drawing: "realistic illustration of the face" ($M = 1.02$, SE = 0.60) and for sketchy drawing: "realization of characteristics of the face" ($M = 2.30$, SE = 1.53).

Table 1
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Activated areas	Naturalistic drawing minus viewing of the face					Sketchy drawing minus viewing of the face			
	Brodmann area	*t*-Value	Coordinates			*t*-Value	Coordinates		
			x	*y*	*z*		*x*	*y*	*z*
Motor areas									
Dorsal premotor cortex (dPMC) right	BA 6	5.43*	36	−6	54	5.68*	24	0	63
dPMC left	BA 6	5.88*	−24	−3	60	6.17*	−30	−12	66
Frontal eye field (FEF) right	BA 6/8	6.93*	30	0	51	3.61	27	15	51
Supplementary motor area									
SMA right	BA 6					8.07*	27	0	57
SMA left	BA 6					4.20	−6	12	51
Primary motor cortex									
M1 right	BA 4	5.54*	60	−15	27				
M1 left	BA 4	5.03*	−36	−15	57	3.92*	−33	−21	57
Cerebellar hemisphere right	Lobule VI	4.85*	15	−51	−18	8.07*	27	0	57
	L VIII					5.98*	39	−66	−33
Somatosensory areas									
Somatosensory cortex right	BA 2	4.88*	36	−39	51	7.71*	33	−42	54
Second somatosensory areas (S II)	OP4	5.54*	60	−15	27	3.44*	63	−18	27
Parietal lobe									
SPL right	BA 7					7.67*	27	−57	48
Ventral intraparietal sulcus		3.70	39	−39	42	6.34*	30	−60	45
Anterior intraparietal sulcus		4.43*	42	−36	48	5.87*	42	−33	48
precuneus						4.34	−15	−60	57
Visual cortex									
Occipital right (OFA)	BA 19	4.90*	21	−63	−15	4.35*	33	−76	35
Broca's area and analogue									
Inferior frontal gyrus left	BA 44	3.78	−54	6	27				
Inferior frontal gyrus right	BA 44					7.10*	57	9	33
Inferior frontal gyrus right	BA 45	4.00	60	18	6	4.55*	45	39	12
Temporal lobe									
Medial temporal (MT)	V5	3.45*	42	−63	3	4.97*	42	−66	3
						5.91*	−39	−63	6
Fusiform gyrus left (FFA)		3.49	−27	−57	−18				
Fusiform gyrus right (FFA)		4.76*	24	−63	−15	4.84*	21	−51	-15
Right inferior temporal						5.20*	45	−63	−6
Right middle temporal						4.97*	42	−66	3
Left middle temporal						5.91*	−39	−63	6

* $p < 0.05$ FWE corrected for selected ROI.

3.2. fMRI-activation

As expected, drawing minus passive viewing of the face showed increased activation in bilateral primary and secondary motor areas, right primary and secondary somatosensory cortex and right cerebellar hemisphere, ipsilateral to the drawing hand. More remarkably, the right occipital lobe was also increasingly involved during drawing. Increased right parietal activation during drawing in comparison to passive viewing was predominantly focused on the superior anterior part of BA 7 and around the intraparietal sulcus. Inferior frontal activation in the right BA 44/BA 45 showed only a significant increase for the sketchy drawing condition. Whereas naturalistic drawing involved increased resources in the right fusiform face area, increased resources for sketchy

Table 2
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Activated areas	Naturalistic drawing minus tracing contours					Sketchy characteristic drawing minus tracing contours			
	Brodmann area	*t*-Value	Coordinates			*t*-Value	Coordinates		
			x	*y*	*z*		*x*	*y*	*z*
V1/V2 left	BA 17/18	6.16*	−18	−63	12	6.92*	−18	−69	18
V1/V2 right	“	5.00*	9	−72	18	3.32	21	−72	15
cuneus right	BA 31	5.39*	6	−72	21	4.00	21	−66	24
cuneus left	BA 31	5.75*	−18	−63	18	4.89*	−15	−72	21
precuneus right	BA 7	5.30*	18	−63	27	4.07	21	−63	24
precuneus left	BA 7	4.39	−12	−66	36				
supplementary motor area (SMA)	BA 6	4.85	12	3	54				
fusiform gyrus right (FFA)	BA 37	3.76	39	−12	−27				
temporal inferior right	BA 21	4.00*	51	−18	−18	3.64	51	−21	−18
parahippocampus		3.33	18	−3	−21				
ventral intraparietal area (VIP)	BA 7					3.79	30	−51	42

* $p < 0.05$ FWE corrected for selected ROI.

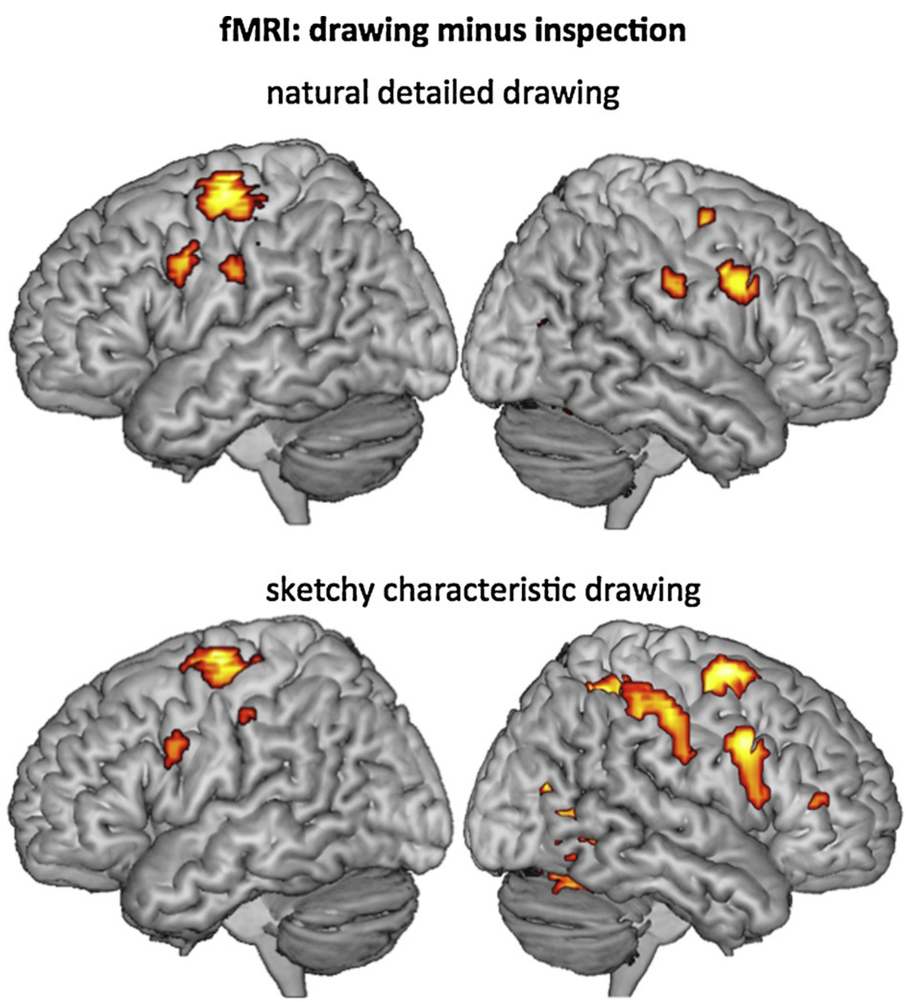

Fig. 2. Functional representation from the contrast with viewing of the face projected on the lateral views of the segmented MNI reference brain with a significance level of $p < 0.001$, uncorrected. Top: naturalistic drawing; bottom: characteristic sketchy drawing. For an exact listing of these representation sites see Table 1.

drawing were also located in more superior temporal areas (see Table 1 and Fig. 2).

The comparison drawing (naturalistic or sketchy) minus tracing with a pencil showed activations predominantly in primary visual areas, the medial occipital and parietal lobe (cuneus and right precuneus). Additional activation was seen in the inferior temporal lobe predominantly right sided (see Fig. 3, Table 2).

Naturalistic minus sketchy drawing showed increased activation in the medial cingulate (MNI-coordinates: 9, 0, 36; $t = 6.76$); sketchy drawing showed no significant increase of activation compared to naturalistic drawing.

4. Discussion

Our aim was to investigate the neural correlates of drawing a portrait including associated motor and sensorimotor processes involved. To this end, we compared drawing naturalistic and sketchy portraits from photos of neutral faces with tracing the contours of the faces with a pencil or passive viewing of the faces in 20 naive participants. We overcame the problem of head movements occurring during actual drawing by constructing a special fMRI compatible table. Thus, we could study a real portrait drawing task allowing for the characteristic alternating gaze pattern between the original and the drawing, and visuo-motor as well as sensorimotor control in an almost natural setting.

Overall, drawing compared to passive viewing did activate the bilateral somatosensory/motor network but did also increasingly recruit areas involved in visual processing located in the right occipital (occipital face area, OFA), MT, and the inferior temporal cortex (fusiform face area, FFA). Areas, which have been associated with attention and selection processes (FEF, cSFS) in the right hemisphere, showed higher activation during drawing than passive viewing of the face as well. Furthermore, increased involvement of vPMC and BA44 point to a recruitment of highly overlearned motor patterns associated with using the pen.

Copying compared to tracing involved the precuneus, the cuneus, and primary visual areas. The precuneus activation presumably resulted from the planning and execution of visually guided hand movements reproducing spatial relations based on working memory.

4.1. Copying vs. passive viewing

Not surprisingly, drawing activated primary and secondary motor areas more strongly than passive viewing. Overall, the motor representations are comparable to those reported in the study of Makuuchi et al. [8], in which the participants had to draw known objects with their fingers. The motor representation during drawing was bilateral and involved predominantly M1, the SMA, and dPMC. However, more pronounced during sketchy drawing, we found a lateralization to the contralateral hemisphere of the drawing hand on the level of the primary motor cortex (M1) and to the ipsilateral side in the anterior cerebellar hemisphere. Anterior cerebellar areas have been described to be predominantly involved in

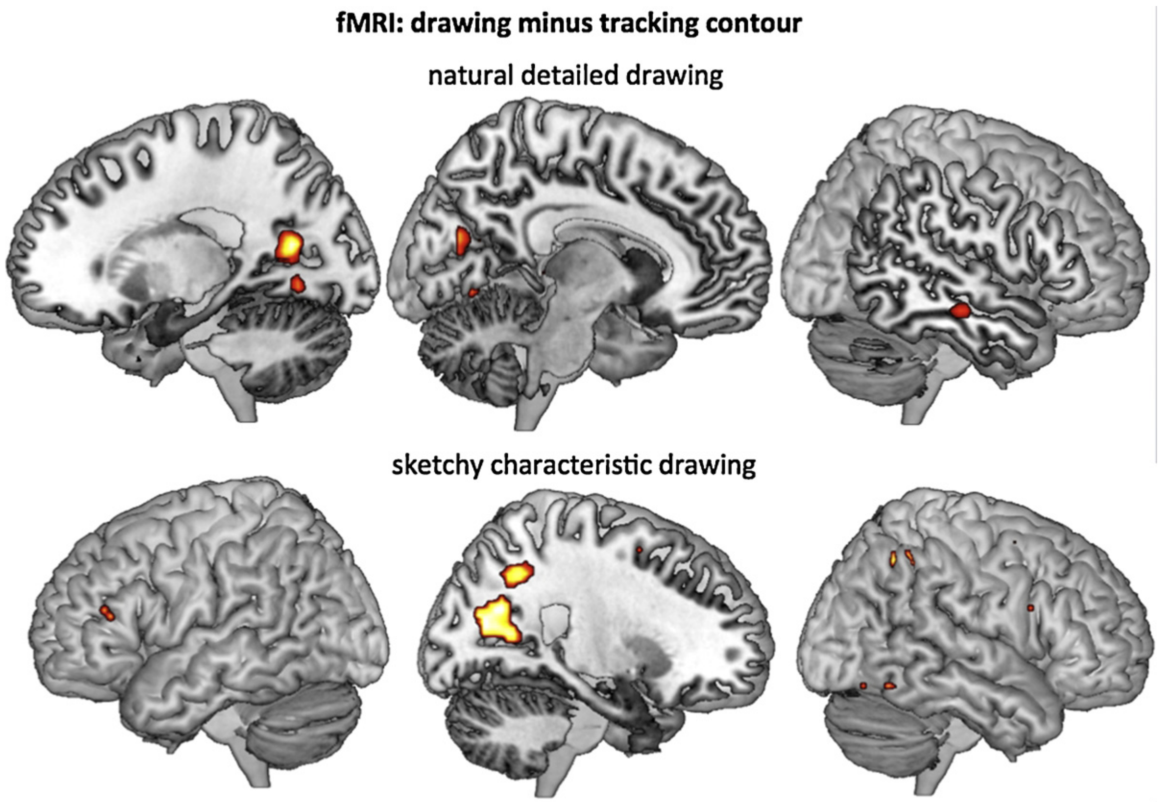

Fig. 3. Functional representation from the contrast with the tracing of the contours of the face projected on medial cuts and lateral views of the segmented MNI reference brain with a significance level of $p < 0.001$, uncorrected. Top: naturalistic drawing; bottom: characteristic sketchy drawing. Positions of slices are provided in the *x*-direction. For an exact listing of these representation sites see Table 2.

somatosensory-motor updating [29–31], which is highly important during both actual drawing and tracing a contour.

Using a pen for drawing engages overlearned movement patterns for reproducing features of the original. Our study and previous studies point to a fronto-parietal network essential for this process. This involves the superior parietal lobe (SPL), ventral premotor cortex (vPMC) together with parts of the inferior frontal gyrus (BA 44, BA 45) both predominantly located in the right hemisphere. These areas are crucially involved in imitation learning (for an overview see [32]) and the vPMC contains neurons processing motor engrams of highly overlearned movements [33]. These activations might therefore reflect the access of highly overlearned movement patterns during working with the pen. Harrington et al. investigated participants during imagined drawing and interpreted observed BA 44 activation as a semantic retrieval because the same area showed activation during writing the name of the object [9]. It might well be that BA44 activation in their task was induced by the imagery task, since it has been shown that BA 44 is highly active even during imagining simple hand movements [25].

The two-fold involvement of vision in drawing brings about eye movements and attention shifts that are in part independent of hand movements, and second, linked to hand movements for visuo-motor guidance. Independent of hand movements, alternating between the original and the drawing [4] was reflected in a bilateral but right lateralized activation cluster encompassing the dPMC, FEF, and the cSFS. Visual processing for face perception activated the right OFA and the right FFA more strongly in drawing than in passive viewing. In both hemispheres these areas are core areas for face recognition [14] but activation in these areas during face perception is usually lateralized to the right side [15]. In a previous mapping study on a linear copying task of cartoon faces, Miall et al. found the FFA and OFA being active as well [3]. Subdividing a face into characteristic elements that can be later reproduced in a motor action is supposed to require detailed analytic visual processing that is not induced by passive viewing. Moreover, a second face was produced during drawing, which presumably increased visual stimulation. Interestingly, MT was increasingly active during drawing, too. This difference was absent if drawing was compared with tracing and therefore probably resulted from visual stimulation by the moving hand.

In our paradigm, eye movements and visual processing during drawing that were independent of hand movements cannot be discerned from those that subserve visuo-motor control. However, previous studies on visually guided reaching and pointing have identified the medial intraparietal sulcus and the dPMC as particularly associated with visuo-motor control of hand movements [20,21]. Thus, the activation of the intraparietal sulcus that was particularly strong for sketchy drawing presumably reflects involvement of the dorsal stream in visuo-motor control.

4.2. *Copying vs. tracing contours*

For drawing contrasted with tracing, we observed bilateral activation in the cuneus and precuneus. The precuneus has multiple functions [34] and can be subdivided in areas with differing functional connectivity [35]. Connectivity data were interpreted to suggest an anterior to posterior division in three functionally separable areas: an anterior area subserving sensorimotor processing, a posterior area involved in visual processing, and a central area connected to dorsolateral prefrontal cortex, the inferior parietal lobule, and the angular gyrus. The central area was ascribed cognitive functions encompassing working memory and action planning. Ventrally adjacent to these precuneus areas, the posterior cingulate is connected to limbic structures in temporal and frontal cortices, and may be responsible for the reported precuneus involvement in episodic memory retrieval.

Among the previous fMRI studies that have reported precuneus activations, which include studies on actual drawing and tracing [3,6,10], presumably those studying visually guided planning of reaching and pointing movements and those studying spatial working memory clarify the critical task demands of copying as opposed to tracing. Precuneus activations have been previously observed when reaching and pointing movements had to be planned to visually encoded targets that were invisible when the movements were executed [22,23,36]. Such planning is required in copying because in copying as opposed to tracing, visually guided hand movements are not directed to visible targets. In copying, hand movements reproduce visual features of the original at locations specified relative to already copied features in the drawing. Thus, higher activation of the precuneus in drawing compared to tracing with a pen is also consistent with the precuneus' involvement in selecting relative locations in spatial working memory [19].

Ferber et al. [6] have also contrasted copying with tracing and have found higher precuneus activation for tracing. Note, however, that their tracing task required following a replay of the participant's previous drawing movements that were shown as a developing line on a screen. Hence, time pressure might have increased the task demands of tracing performed as tracking with coordinated eye and hand movements [37] or the replay may have induced episodic memory retrieval.

Higher activation in primary visual areas in copying as opposed to tracing presumably resulted from both more analytic visual processing while copying and additional visual stimulation.

4.3. Naturalistic vs. sketchy drawing

In amateurs the two different ways of drawing a portrait did not reveal substantial differences. Behaviorally, limited quality reflected in ratings of the drawings suggest that the participants were not capable of performing a differentiated drawing technique. Only medial cingulate gyrus was more strongly involved during naturalistic than during sketchy drawing when both were directly contrasted, which might reflect an increased monitoring effort during creating a more detailed drawing [3]. In the contrasts comparing drawing with passive viewing, higher SMA and cerebellar activations were observed for sketchy drawing. Probably, these reflect the higher speed of movement during sketchy drawing [10].

4.4. Conclusion and outlook

In the present study we identified neural correlates of different aspects of drawing a portrait in an almost natural setting. Copying involves visual analysis reflected in activation in face specific perception areas located in the right occipital and inferior temporal gyrus. Eye movements and attentional selection processes activated the FEF and cSFS. Copying furthermore requires vision for action to guide the application of motor patterns. Visuo-motor control recruited dPMC and posterior parietal areas including the ventral intraparietal sulcus. Cortical areas processing motor engrams necessary for overlearned motor processes during usage of the pen were identified in the right ventrolateral prefrontal gyrus. Right cerebellar lobe and right anterior SPL activation point to sensorimotor control of motor performance and somatosensory processing. The precuneus activation observed for copying as opposed to tracing presumably resulted from the demands to plan visually guided hand movements in correct spatial relations based on spatial working memory. In amateurs, naturalistic and sketchy drawing hardly differed. Yet, we expect to find differences in a group of more experienced drawers with this paradigm that retains the features of an actual complex drawing task.

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