



The artist emerges: Visual art learning alters neural structure and function



Alexander Schlegel^{a,*}, Prescott Alexander^a, Sergey V. Fogelson^a, Xueting Li^{a,b}, Zhengang Lu^a, Peter J. Kohler^a, Enrico Riley^c, Peter U. Tse^a, Ming Meng^a

^a Dartmouth College, Department of Psychological and Brain Sciences, Hanover, NH 03755, USA

^b Beijing Normal University, National Key Laboratory of Cognitive Neuroscience and Learning, Beijing 100875, China

^c Dartmouth College, Studio Art Department, Hanover, NH 03755, USA

ARTICLE INFO

Article history:

Accepted 7 November 2014

Available online 15 November 2014

Keywords:

Art
Creative cognition
Perception
Perception-to-action
Plasticity
White matter
Cerebellum
Motor cortex
DTI
fMRI
MVPA

ABSTRACT

How does the brain mediate visual artistic creativity? Here we studied behavioral and neural changes in drawing and painting students compared to students who did not study art. We investigated three aspects of cognition vital to many visual artists: creative cognition, perception, and perception-to-action. We found that the art students became more creative via the reorganization of prefrontal white matter but did not find any significant changes in perceptual ability or related neural activity in the art students relative to the control group. Moreover, the art students improved in their ability to sketch human figures from observation, and multivariate patterns of cortical and cerebellar activity evoked by this drawing task became increasingly separable between art and non-art students. Our findings suggest that the emergence of visual artistic skills is supported by plasticity in neural pathways that enable creative cognition and mediate perceptuomotor integration.

© 2014 Elsevier Inc. All rights reserved.

Introduction

Art is a complex and uniquely human phenomenon. The creation of artistic work has historically been a mysterious and poorly understood process, often even by artists themselves (Stiles and Selz, 2012). However, according to central tenets of neuroscience, the work of an artist must be mediated by the brain. How does the brain support the cognitive skills necessary to create art?

Art has appeared in many forms throughout human history. The qualities that distinguish artistic work are thus often difficult to define. For example, while some *trompe l'oeil* painters such as William Harnett (Frankenstein, 1953) attain an astounding ability to recreate visual scenes accurately, representation for other painters such as abstract expressionist Barnett Newman (Shiff, 2004) is less important than the concepts or processes that their works communicate. Nonetheless, most artists, regardless of their motivation or medium, spend years developing patterns of thought and behavior that lead ultimately to expression in a work of art. Here, we focused narrowly on a single type of artwork: representational, two-dimensional visual depictions created from observation. We

necessarily ignored many important factors such as social, cultural, and affective contexts that are vital to the work of many artists (cf. Stiles and Selz, 2012). No single study can address every factor that influences artistic skill. However, the results presented here may provide a window into some of the neural processes that endow humans with a seemingly limitless ability to create new objects, ideas, and processes.

In the current study we investigated how artistic behaviors are learned, focusing on representational visual art and on three areas of cognition that are relevant to many visual artists: creative cognition, visual perception, and perception-to-action (Fig. 1A). We asked how skills associated with each of these three cognitive domains change and how the brain reorganizes as students learn to create visual art. We recruited 35 undergraduate college students for monthly testing; 17 of these participants took a 3-month-long introductory observational drawing or painting course offered by the Studio Art Department at Dartmouth College, while 18 control participants did not study art. All participants attended monthly MRI scanning sessions. Below we introduce the three areas of cognition that we studied and their potential relevance to visual art.

Creative cognition

Artists are distinguished by the ability to think in new ways, developing new patterns of and connections between ideas to imagine and

* Corresponding author at: Department of Psychological and Brain Sciences, H. B. 6207, Moore Hall, Dartmouth College, Hanover, NH 03755, USA. Fax: +1 603 646 1419.
E-mail address: schlegel@gmail.com (A. Schlegel).

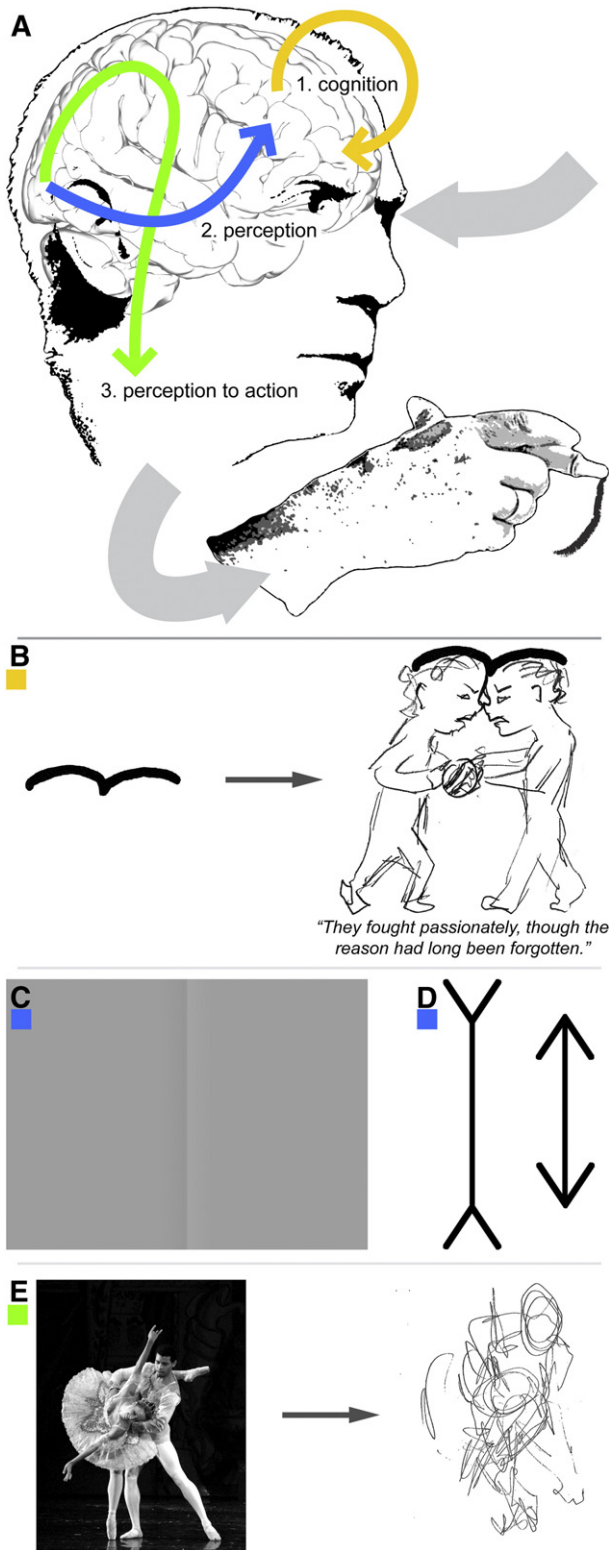


Fig. 1. Experimental design. A. Areas of cognition important to the production of representational visual art: creative cognition, perception, and perception-to-action pathways. B. Example prompt and participant response from the TTCT. Participants were instructed to draw something that no one else would think of, to tell as rich and complete a story as possible, and to give each response a creative title. C. The Craik–O’Brien–Cornsweet illusion, in which a dark-to-light gradient heading left of center and a light-to-dark gradient heading right of center cause a uniform gray rectangle to appear darker on the left side than on the right side. D. The Müller–Lyer illusion, in which a line segment with outward facing arrow ends appears longer than an identical-length line segment with inward facing arrow ends. E. Example stimulus and participant response from the gesture drawing task. Participants had 30 s to complete a gesture drawing of the observed human figures.

create artifacts and processes that have never existed previously. The sources of this creativity are among the least understood and most mythologized aspects of art production (Milbrandt and Milbrandt, 2011; Taylor, 1976). Creative cognition is notoriously difficult to define within a scientific context, partly because creativity can be manifested in myriad domains such as artistic and scientific fields, verbal and visual modalities, and divergent and convergent thought (Dietrich and Kanso, 2010). Many questions about what makes artists creative remain open, especially with respect to the brain's role in these creative processes. Previous neuroscientific studies have used a range of approaches to study the neural basis of creativity in artists, but little consensus about this basis has emerged. For example, Bhattacharya and Petsche (2005) used EEG to study differences in cortical activity between artists and non-artists as both produced drawings of their own choice and found differences in short and long range neural synchronization patterns between the two groups. Kowatari et al. (2009) asked design experts and novice participants to invent a new type of pen while undergoing functional MRI (fMRI) scans and found that creative output was correlated with the degree of dominance of right over left prefrontal cortical activity. Limb and Braun (2008) used fMRI to show that jazz pianists experienced extensive deactivation of prefrontal cortex when they played improvised compared to over-learned musical pieces. Solso (2001), on the other hand, found reduced activity in the parietal cortex in a skilled portrait artist compared to a novice participant as both produced drawings of faces. While little consensus has emerged from such studies, the many emerging findings about both artists and creative cognition more generally have shown that creativity is a complex rather than monolithic process and that researchers must therefore avoid the tendency to reduce creativity to simple conceptual constructs (Arden et al., 2010; Dietrich and Kanso, 2010; Hee Kim, 2006). Thus, in this study we chose assessments of creativity (described below) that measured many aspects of creative ability.

A recent study by Jung et al. (2010) investigated the relationship between white matter organization and creative cognitive ability using diffusion tensor imaging (DTI). They found an inverse correlation in the frontal lobes between fractional anisotropy (FA; a measure of the directionality of water diffusion in white matter) and both divergent thinking and openness, such that more creative individuals as measured by these traits tended to have lower frontal white matter FA. While FA is often associated with myelination of axons, several other properties such as axon count, axon packing, and crossing fibers can affect the anisotropy of water diffusion in the brain as well. While the exact neural correlates of FA are not determined precisely, DTI nonetheless provides a non-invasive means of investigating longitudinal changes in the structure of white matter. Several recent studies have shown that diffusion tensor imaging (DTI) is an effective tool for tracking learning-related changes in the white matter organization of the brain in as little as six weeks or as long as nine months (May, 2011; Schlegel et al., 2012; Scholz et al., 2009). Even shorter term changes (in as little as five days) have been observed in brain structure using other imaging modalities (Ditye et al., 2013; Driemeyer et al., 2008).

Visual perception

The visual system is organized to recover intrinsic properties of perceived objects such as size and reflectance. It therefore often counteracts context-dependent aspects of objects such as distance from the observer and ambient luminance (Todorović, 2002). In other words, the brain constructs our perception of the world not necessarily in accordance with the physical stimulation, but rather as it infers things to be intrinsically. For instance, a white flower still appears white in a blue-lit room, even though the flower reflects only blue light in such a room. While such inferences on the part of the visual system permit us to perceive intrinsic properties of objects (e.g. size, shape, or pigment), they can also lead to illusory percepts such as the Craik–O’Brien–Cornsweet and Müller–Lyer illusions (Figs. 1C & D) (Müller-Lyer, 1889; Todorović, 1987).

One skill acquired by many visual artists is the ability to create precise, realistic representations of the world. For these representations to appear realistic, they must reflect accurately the physical, rather than the inferred, properties of the observed environment. A representational artist may therefore need to counteract these inferences. Otherwise, the brain's corrections would propagate to the artwork and result in incorrect depictions of the subject matter (e.g. in a painting of a white flower in a blue-lit room, the flower would look whiter than in real life). How do representational artists learn to bypass these seemingly automatic inferential processes? Do their brains reorganize so as to perceive the true physical properties of stimuli directly, or do artists use other cognitive strategies such as correcting inaccuracies in an artwork by comparing the actual stimulus with an initial attempt at its representation? Previous studies have presented conflicting findings in this regard. Graham and Meng (2011) reported that professional painters were less susceptible than non-artists to the Craik–O'Brien–Cornsweet effect, suggesting that these artists' direct perceptual experience of luminance had changed as a result of training and practice. However, Perdreau and Cavanagh (2011) found no differences between the abilities of visual artists and non-artists to overcome luminance and size constancy operations. Drawing ability, rather than artistic ability more generally, has been shown to affect size constancy processes (Ostrofsky et al., 2012), integration of object information (Perdreau and Cavanagh, 2013), and encoding of object structure (Perdreau and Cavanagh, 2014). Several other scholars have argued both for and against differences between the perceptual abilities of artists and non-artists (Fry, 1920; Gombrich, 1960; Kozbelt and Seeley, 2007; Ruskin, 1857; Thouless, 1932). How representational artists can create faithful depictions of environments that are filtered through perception is therefore still an open question.

Perception-to-action

No matter the style or medium in which they work, artists must develop the ability to translate thoughts and perceptual experiences into skilled actions; in this case, drawing and painting. Here we conceive of perception-to-action as encompassing those cognitive processes that involve close interactions between perceptual and motor processes, broadly defined. Relevant perceptual processes could include visual perception of the subject of an art work or of the artist's own hand, or proprioceptive feedback from hand and arm as a drawing is created. Relevant motor processes could include both the hand and arm movements that create the art work and the eye movements that direct attention over the subject.

Previous studies have investigated how the drawing habits and abilities of artists differ from those of non-artists. Kozbelt (2001) found that artists' superior skills in perception, motor actions, and perceptuomotor integration contribute to their advantage in drawing ability. His data indicated additionally that the perceptual advantages among artists had developed largely to serve drawing skills. Providing further evidence for a tight integration between perception and action among artists, Cohen (2005) found that artists shift their eyes between the drawing and its subject more frequently and that this gaze frequency correlates with drawing accuracy. He suggested that frequent eye gaze shifts to update the contents of perception allow artists to reduce the amount of (possibly inaccurate) information held in working memory. Glazek (2012) found additionally that artists engage more efficient visual encoding and motor output mechanisms when drawing. These results may also relate to Perdreau and Cavanagh's (2011) argument that artists overcome constancy operations essentially by trial and error: drawing a subject and then making corrections after comparing the drawing to the subject. If this is the case, one aspect of becoming skilled in drawing may be development of the ability to compare drawing and subject while creating an artwork.

An influential model of the visual system proposes that visual information processing can be divided primarily along two neural pathways

or processing streams (Goodale and Milner, 1992; Mishkin and Ungerleider, 1982). The ventral or *vision for perception* stream is responsible for recovering information about object identity and tracks features such as size, shape, and color. The dorsal or *vision for action* stream is responsible for spatial awareness and the guidance of movements such as the strokes of a paintbrush. Since artists' perceptual skills exist to subservise skilled movements, it is possible that a representational visual artist's training can target the functions of the *vision for action* stream over those of the *vision for perception* stream. If so, finding evidence of differences between the perceptual skills of artists and non-artists may depend on whether the tests of those skills target purely perceptual or perception-to-action pathways.

In the current study we investigated behavioral and neural changes in creative cognition, visual perception, and perception-to-action as follows. First, in behavioral sessions at the beginning and end of the study, participants completed the Torrance Tests of Creative Thinking Figural Form A (TTCT; Fig. 1B) (Torrance, 1969). The TTCT tests for the ability to think creatively as defined by several factors such as fluency, originality, abstractness of thought, the ability to depict complex systems compellingly, and the creative use of imagery and language. The test yields a single composite creativity index (CI) as well as submeasures that separately assess many aspects of creative ability. Although the painting and drawing courses completed by the participants were not designed explicitly to improve the creative qualities measured by the TTCT, we hypothesized that training in painting and drawing would transfer to improvements in some or all of these qualities. Because of the finding of Jung et al. (2010) we hypothesized additionally that any changes we observed in the creative thinking abilities of our experimental group would correlate with corresponding changes in prefrontal white matter organization.

Second, in order to track the development of perceptual abilities in our visual art students and test whether improvements in these abilities entail changes in the activity of the brain's perceptual pathways, we acquired a series of functional scans in each session while participants judged properties of illusory visual stimuli. For illusory stimuli we used the Craik–O'Brien–Cornsweet illusion (Fig. 1C) and the Müller-Lyer illusion (Fig. 1D). We chose these two classic visual illusions because they are cognitively impenetrable. Previous neuroimaging studies have shown that brain areas implicated in early and mid-level visual processing underlie the illusory effects (Perna et al., 2005; Plewan et al., 2012). If perceived strengths and neural correlates of these visual illusions change as students become artists, it would suggest neural plasticity at perceptual processing levels. However, no changes in earlier levels of processing would suggest that artists may have learned to interpret the outputs of early processing differently.

Finally, to assess learning-related changes in perception-to-action pathways, we acquired a functional scan during each session in which participants made quick, 30 second gesture drawings based on observation of human figures (Fig. 1E). Gesture drawing is a technique often used among representational artists to develop more direct translation of visual observation to hand and arm movements. In creating gesture drawings, one is often discouraged from devoting attention to the art work itself, focusing more on translating directly from the perceived form and gesture to motor actions that faithfully capture those aspects of the subject on the canvas. This was especially true in the current study, since participants lay with their heads still in the scanner and had little opportunity to see the drawings as they were produced. If visual art training targets perception-to-action, we hypothesized that changes in neural activity would be observed in the corresponding perceptuomotor pathways among our art students.

Until recently, plastic reorganization of the brain was thought to occur mainly during childhood and adolescence, leaving adults with limited means to learn new skills. Research in the last two decades has convincingly overturned this belief, revealing a brain that remains able to reorganize with learning well beyond early developmental periods (Draganski et al., 2004; Lövdén et al., 2010; May, 2011; Schlegel

et al., 2012; Scholz et al., 2009; Taubert et al., 2010). Structural changes in the adult brain have been observed with interventions lasting as little as six weeks (Draganski et al., 2004). Our previous work has shown that novel insights can be gained into the neural processes underlying specific behaviors by studying how the adult brain changes as those behaviors are learned (Schlegel et al., 2012). Thus, studying how the brain changes as students become artists may reveal insights into how the brain mediates artistic work.

Materials and methods

Participants

Prior to participating, 45 participants (26 females, aged 19–22 years) with normal or corrected-to-normal visual acuity gave informed written consent according to the guidelines of Dartmouth College's Committee for the Protection of Human Subjects. Data from 10 participants who withdrew before completion of the study were discarded before further analysis. Our final study cohort consisted of an experimental group of 17 undergraduate students (13 females, aged 18–22 years) who completed a three-month-long course in either introductory drawing or introductory painting, and a control group of 18 undergraduate students (9 females, aged 19–22 years) who did not study art. Participants were recruited for the study during the first week of courses, and we therefore did not control the group assignment. Control participants were recruited from a group of students taking an introductory organic chemistry course. Our strategy was to choose a control group that engaged in an equally intensive course of study, but within a system that required closed rather than open-ended solutions. While no significant differences in gender, age, handedness, or grade point average existed between the two groups (Table S1), we were not able to precisely match these characteristics because of the nature of the group assignment.

Drawing & painting courses

Experimental participants completed either an introductory course in observational drawing, or a similar course in painting for which the drawing course was a prerequisite. Both courses were 11 week, undergraduate-level classes offered for credit through the Studio Art Department at Dartmouth College. Classes met for 4 h each week, with approximately 15–20 additional hours spent on work per week outside of class. The purpose of the introductory drawing course was to develop technical and expressive drawing abilities in terms of line, scale, space, light, and composition. Work was primarily observational, although non-observational drawing was also explored. The painting course further developed the topics from the drawing course, and also addressed paint application and color theory, mixing, and composition. Both courses focused additionally on the development of artistic expression and on the critical analysis of art works. Detailed course descriptions are provided for both courses as supplemental text.

Procedure

Participation consisted of two half-hour-long behavioral sessions, one at the beginning and one at the end of the study, during which participants completed the Torrance Tests of Creative Thinking (TTCT) Figural Form A, and four one-hour-long magnetic resonance imaging (MRI) sessions, one per month, during which we collected several functional and structural scans. Functional data were collected as participants performed two types of behavioral tasks. In the first task, participants made judgments about the physical characteristics of visual illusion stimuli. In the second task, participants produced gesture drawings based on observation of photographs of human models. These tasks are described in further detail below. DTI data were collected as participants rested but lay still in the scanner.

TTCT task

The TTCT Figural Form A is a timed 30 min, standardized pencil and paper test of creative thinking. The test consists of three 10 minute activities in which participants are instructed to complete partially drawn figures by thinking of things no one else would think of and by telling as creative and elaborate a story as possible (e.g. Fig. 1B). Participants took the TTCT twice, once at the beginning and once at the end of the study.

Illusion task

Stimuli were modeled after the Craik–O'Brien–Cornsweet illusion (Fig. 1C) and the Müller–Lyer illusion (Fig. 1D), with actual differences introduced in luminance and length, respectively. In a given trial, an illusory stimulus was presented for 1 s and the participant had 2 s from stimulus onset to indicate which side was either brighter (for the Craik–O'Brien–Cornsweet or “luminance” task) or longer (for the Müller–Lyer or “length” task) before the next stimulus appeared. The Craik–O'Brien–Cornsweet illusion stimulus measured 22.72° of visual angle wide and 17.14° tall, while each center gradient was 3° wide. The Müller–Lyer line segments were oriented vertically and centered on the screen, with a 4° horizontal separation between them. Line segments ranged in length from 4° to 8°. The gradient directions and lighter side for the luminance task and the arrow end direction and longer side for the length task were counterbalanced across trials, and participants were not given feedback on their responses. During each session, participants completed one fMRI run of each illusion task. A run consisted of five blocks of 20 trials each, yielding 100 trials per task, participant, and session. Blocks were interleaved with 12 second rest periods.

Gesture drawing task

Stimuli consisted of grayscale photos of human figures in various poses (e.g. Fig. 1E). Before the first scan, participants were shown examples of gesture drawings and instructed that gesture drawing is an activity in which fluid, continuous strokes are used to build up the form and movement of the observed figure quickly rather than to capture fine details. In each trial, a figure was shown to the participant who then had 30 s to complete a gesture drawing of that figure. Participants used a #2 pencil while lying supine in the scanner and resting a wedge-shaped drawing pad and paper on their abdomens. Because of their position and the instruction to keep their head still during scans, participants had little opportunity to view the gesture drawings as they were produced. This constraint was not a major concern because, as discussed above, gesture drawing technique stresses that attention be maintained on the subject rather than the art work. An experimenter stood at the side during the scan to provide a new piece of paper in between drawings. During each session, participants completed one fMRI gesture drawing run, consisting of 10 drawings interleaved with 14 second rest periods.

MRI acquisition

MRI data were collected using a 3.0-Tesla Philips Achieva Intera scanner with a 32-channel sense head coil located at the Dartmouth Brain Imaging Center. T2*-weighted gradient echo planar imaging scans were used to acquire functional images covering the whole brain (2000 ms TR, 20 ms TE; 90° flip angle, 240 × 240 mm FOV; 3 × 3 × 3.5 mm³ voxel size; 0 mm slice gap; 35 slices). One T1-weighted structural image was collected each session using a magnetization-prepared rapid acquisition gradient echo sequence (8.176 ms TR; 3.72 ms TE; 8° flip angle; 240 × 220 mm² FOV; 188 sagittal slices; 0.9375 × 0.9375 × 1 mm³ voxel size; 3.12 min acquisition time). One diffusion-weighted scan was collected each session to acquire diffusion tensor imaging (DTI) data (32 directions; 1000 s/mm² b-value; 8.379

s TR; 73.49 ms TE; 90° flip angle; 224 × 224 mm² FOV; 70 axial slices; 2 × 2 × 2 mm³ voxel size; one additional b = 0 s/mm² image; 2 signal averages per volume; 10.47 min acquisition time).

MRI data preprocessing

fMRI and DTI data were preprocessed using FSL (Smith et al., 2004). Functional data were motion and slice scan time corrected, temporally high pass filtered with a 1/100 Hz cutoff, and spatially smoothed with a 6 mm full-width-at-half-maximum Gaussian kernel. For each DTI data set, fractional anisotropy (FA), radial diffusivity (RD), axial diffusivity (AD), and mean diffusivity (MD) were reconstructed, z-transformed to reduce the effect of potential unexpected changes in equipment function over time, and normalized to a standard 2 × 2 × 2 mm³ template in Montreal Neurological Institute (MNI) space via FSL's FNIRT non-linear registration tool. High-resolution anatomical images were processed using the FreeSurfer image analysis suite (Dale et al., 1999).

DTI data analyses

Our DTI data analyses followed the procedure from Schlegel et al. (2012).

Whole-brain GLM

A cross-subject longitudinal GLM analysis using FSL's *randomise* tool was performed on the whole-brain FA data (5000 permutations, within-subject only). Data from all four sessions were included in the analysis. Only data from white matter were analyzed, as determined individually for each participant by FreeSurfer's automatic segmentation algorithm. Additionally, each voxel location in MNI space was only included in the analysis if at least 75% of participants had white matter at that location. Even for locations that passed the 75% threshold, data from non-white matter at those locations were excluded from the analysis. This process allowed for as much of the white matter data as possible to be included without risking errors due to potential misregistration between white and non-white matter regions. Included in the GLM design matrix were predictors to account for existing differences between participants and predictors for time, separated by group. *t*-contrasts were defined to assess group by time interaction effects, and the resulting statistical maps were threshold-free cluster enhanced and false discovery rate (FDR) corrected for multiple comparisons (Smith and Nichols, 2009). The same analysis was also performed for RD, AD, and MD measures.

Time course

For each participant, the same GLM as in the whole-brain longitudinal DTI analysis was performed with that participant's data left out. The participant's FA data at voxels with $p \leq 0.05$ (uncorrected) in the group by time interaction contrast of this analysis were then averaged to compute one mean FA value for that participant at each time point. Uncorrected *p* values were used in this voxel selection procedure to maximize the amount of meaningful data included in the time courses, while excluding the data to be averaged from the voxel selection step prevented type I errors in the GLM analysis from propagating to the time courses (i.e. decreasing the slope of the participant group and increasing the slope of the control group artificially). Results for each participant were converted to percent change from the $t = 0$ value of a best-fit line for that participant's data, and these time courses were then averaged by group and shown in Fig. 3B.

Structural MRI data analysis

The same whole-brain longitudinal GLM analysis as described for the DTI data analyses was performed on gray matter thickness data as reconstructed by FreeSurfer.

TTCT data analyses

Behavioral

The TTCTs were scored independently and blindly according to standard rating procedures (see Torrance, 1969) by two independent raters who also evaluated the gesture drawings (described below). Inter-rater reliability was excellent ($\alpha = 0.94$ for the composite creative index [CI]). The group by time interaction term of a two-way, repeated measures ANOVA evaluated whether the change in CI over the study differed between the two groups. A factor analysis was performed on all TTCT subscores including a modification of the *checklist of creative strengths* in which the total number of instances of each checklist item was recorded for each test section. Factors were extracted based on principal components with eigenvalues greater than 1 and varimax rotated (resulting in the five factors shown in Fig. 2B). Additional one-tailed, unpaired *t*-tests evaluated whether each of these factors increased more in the experimental group than the control group over the study period. *p*-Values were FDR corrected for the five comparisons.

Correlation with DTI data

For each identified TTCT factor, a between-subject correlation analysis was performed comparing the change in factor score between the two test administrations and the slope of the FA changes calculated above. For Factor 2, which showed a significant result in this analysis, the same correlation analyses were performed between FA slope and the change in the four TTCT subscores that loaded highly (coefficient ≥ 0.4) onto this factor. The resulting *p*-values were FDR corrected for multiple comparisons across the four submeasures.

Illusion data analyses

Behavioral

We reconstructed a psychometric curve for each fMRI illusion run by fitting a Weibull function to participant responses for that run. Responses were coded for the Craik–O'Brien–Cornsweet luminance task based on whether the participant chose the side with the lighter or darker gradient and for the Müller–Lyer length task based on whether the participant chose the arrow with the outward or inward facing ends. The *t* parameter from the Weibull fit gives an estimate of the point of subjective equality (or the actual luminance or length difference that led the participant to make each choice with equal probability) and hence the strength of the illusory effect. The *b* parameter from the fit determines the steepness of the psychometric curve and thus indicates the consistency of the participant's decision criterion. The group by time interaction terms from longitudinal linear mixed model (LMM) analyses were used to determine whether the trajectory of these two parameters differed between the two groups over the study period.

fMRI univariate

A whole-brain longitudinal GLM analysis was carried out for each illusion task to determine whether brain activity changed differentially between the two groups during the study. Only data from cortical gray matter and subcortical structures were analyzed, as determined by FreeSurfer's automatic segmentation algorithm (Dale et al., 1999). A first-level GLM in FSL's FEAT tool for each participant and session used a boxcar predictor to model differences in blood-oxygenation level dependent (BOLD) measurements between task and rest, convolved with a double-gamma hemodynamic response function (Smith et al., 2004). The model parameter estimates from this analysis were passed to a higher-level longitudinal GLM analysis using FSL's *randomise* tool (5000 permutations, within-subject only), like that used for the DTI analysis described above. *t*-Contrasts were defined to assess group by time interaction effects, and the resulting statistical maps were threshold-free cluster enhanced and FDR corrected for multiple comparisons.

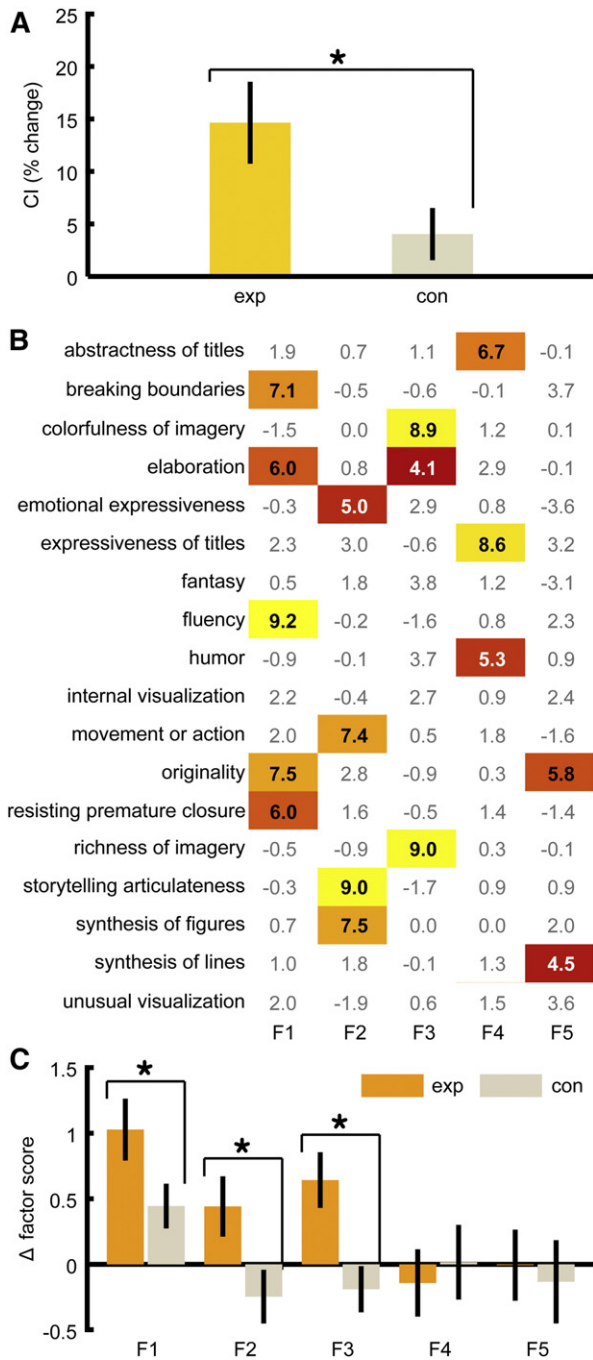


Fig. 2. Results of creative thinking analysis. Asterisks indicate significance. Error bars indicate standard errors of the mean. **A.** Art students increased in creative thinking ability compared to the controls, as measured by the TTCT composite creative index. **B.** A factor analysis of the 18 TTCT submeasures revealed five factors that accounted cumulatively for 59.7% of variance in the participant responses. Factor loadings for each submeasure are shown, multiplied by 10 for presentation. Loadings with magnitude greater than 0.4 are highlighted and color coded by increasing magnitude (red to yellow). **C.** Scores for Factors 1 through 3 increased in art students relative to controls, indicating that art students improved in their ability to think divergently, model systems and processes, and portray imagery. *p*-Values are FDR corrected for the five comparisons.

fMRI multivariate

Multivariate pattern classifications were carried out using PyMVPA (Hanke et al., 2009; see Norman et al., 2006 for a detailed introduction to multivariate classification analysis). For each session we performed a whole-brain, cross-subject multivariate classification analysis, in which we trained a machine classifier to distinguish between experimental and control participants based on patterns of brain activity

measured during the gesture drawing task. We used a whole-brain classification procedure rather than a searchlight analysis for two reasons. First, searchlight analyses are only sensitive to localized patterns of information, since each classification is performed only on a localized cluster of voxels. A whole-brain classification allows patterns to be distributed across the brain, as might be expected for complex cognitive processes. Second, searchlight analyses entail a large number of multiple comparisons that can be avoided by performing a single whole-brain classification. As classification data we used the parameter estimates (i.e. “beta values”) from the first-level univariate analysis described above. These parameter estimates represent the change in brain activity in each voxel while drawing, compared to rest. During classification, the machine classifier is first trained by providing it with a set of patterns along with the associated labels (in this case “experimental” or “control”). After training, the classifier is tested by giving it a new pattern that was held out of the training step and determining whether it can assign the correct label to that pattern. This training/testing step is repeated in a cross-validation procedure in which each pattern is successively held out of the training data and included in the testing data. If the classifier can label the test patterns correctly above chance over all of the cross-validation folds, then information exists within the patterns that distinguishes the two groups. In a whole-brain classification, an initial voxel selection procedure is conducted to determine a subset of voxels in the whole cortex to include in the classification. Specifically, in each fold of the cross-validation we first performed a one-way ANOVA between the two groups’ parameter estimates (leaving out data from the held out participant). The 1% of voxels with the highest *F*-scores in this ANOVA were then selected for training and testing. This selection procedure allowed us to reduce the dimensionality of the multivariate patterns in a principled way while not biasing the classification results, since the testing data were left out of the selection mechanism. One limitation of the whole brain classification selection procedure is that it may discard voxels that still contain information that distinguishes the two groups, but not enough to pass the selection threshold (i.e. not showing large enough between group differences). The selection threshold we chose, however, allowed us to strike a balance between finding information if it was present and avoiding overfitting of the data. We used a linear support vector machine (SVM) as our classification algorithm, and leave-one-subject-out cross validation (i.e. one participant’s data were held out from the training set in each cross-validation fold). Because the training data were unbalanced between groups, we included an additional step in which the classifier was trained and tested 10 times for each cross-validation fold, using a random subset of balanced data for training. The classifier performance for each fold was then calculated as the average performance across those 10 subfolds. Classification accuracies from these analyses were compared to chance using one-tailed Monte Carlo tests with 1000 permutations.

Gesture drawing data analyses

Behavioral

All gesture drawings were digitized and scored independently and blindly by two trained raters. One rater was a visual artist who was not familiar with the participants’ artwork and the other was a research assistant who was trained by the first rater. The score for each drawing was an integer between 1 (lowest quality) and 10 (highest quality), based on an assessment of line quality, resemblance to the figure, and expressiveness of the depicted gestures. The inter-rater reliability was excellent ($\alpha = 0.82$). The group by time interaction effect from an LMM analysis was used to determine whether the change in these ratings differed between the two groups over the study period.

fMRI

To evaluate whether differences in head movement could have led to our observed effects, we conducted two-tailed, unpaired *t*-tests

between the two groups for each session using the per-run mean relative displacement as reported by FSL's MCFLIRT tool. Univariate and multivariate analyses were carried out on the gesture drawing fMRI data as in the illusion analyses described above. To confirm that the above-chance multivariate classification accuracies observed were not due to gross BOLD level differences between the two groups, an additional higher-level univariate whole-brain GLM analysis was performed for each session using *randomise* (5000 permutations, threshold-free cluster enhanced and FDR corrected for multiple comparisons), with *t*-contrasts defined to evaluate between-group BOLD differences. As an additional control to confirm that the effects we observed were due to fine-scale patterns of activity, the same multivariate analysis was performed using the mean pattern values as samples rather than the patterns themselves.

Results

Creative cognition

In behavioral sessions at the beginning and end of the three month study period, participants completed the TTCT Figural Form A, a test of conceptual creativity. All tests were scored independently and blindly by two trained raters. The inter-rater reliability was excellent ($\alpha = 0.94$). For each participant, we calculated the change between the two sessions in the composite creative index (CI) given by the TTCT (Fig. 2A). A two-way, repeated measures ANOVA comparing the absolute TTCT CI scores showed a significant interaction between group and time, indicating that the art students' creative thinking ability improved significantly compared to control participants during the study ($F(1,32) = 4.47, p = 0.0423$). Note that differences between the two groups' CI measures existed at the first session ($t(32) = -3.85, p < 0.001$; see Table S2). Because creativity is a complex trait (Dietrich and Kanso, 2010; Hee Kim, 2006), reducing creative cognition to a single quantity such as CI would limit our understanding of the changes that occurred. CI is actually derived from 18 different submeasures of creativity (see Fig. 2B), so we performed a factor analysis on these submeasures in order to extract multiple dimensions along which to examine the changes that occurred among our participants. This analysis yielded five factors that together explained 59.7% of the variance in the TTCT data (Fig. 2B). The submeasures *fluency*, *originality*, *breaking boundaries*, *elaboration*, and *resisting premature closure* loaded highly onto Factor 1. These submeasures all target divergent thinking, defined as the ability to produce many (*fluency*, *elaboration*) original (*originality*, *breaking boundaries*, *resisting premature closure*) solutions to a problem (Guilford, 1967). *Storytelling articulateness*, *synthesis of figures*, *depicting movement or action*, and *emotional expressiveness* loaded highly onto Factor 2. These submeasures all required the modeling of a system or process (story narratives, the continuation of a theme over multiple panels, movements and actions, and emotional states). *Richness of imagery*, *colorfulness of imagery*, and *elaboration* loaded highly onto Factor 3 and shared a common theme of requiring the depiction of rich, complex, effective imagery. *Expressiveness of titles*, *abstractness of titles*, and *humor* loaded highly onto Factor 4, with the common theme of involving verbal creativity. And *originality* and *synthesis of lines* loaded highly onto Factor 5, with no discernible interpretation.

We calculated the change in each of these five factor scores for each participant and performed one-tailed, unpaired *t*-tests between the experimental and control groups to determine which factors were responsible for the improvements in creative thinking among the art students. The results of this analysis showed that art students improved over controls in the creative qualities captured by Factors 1, 2, and 3 (divergent thinking, modeling of systems and processes, and imagery; Fig. 2C; Table S3). Factors 4 and 5 showed no significant changes between the two participant groups.

In order to assess whether these improvements in creative ability related to changes in white matter structure, we first performed a whole-

brain (white matter only), permutation-based longitudinal GLM analysis on the Fisher's Z transformed fractional anisotropy (FA) values derived from the DTI scans collected for each participant and session. FA quantifies the degree to which the diffusion of water is biased in particular directions and is associated with variations in axon count and diameter, density of axonal packing, myelination, and the coherence of axon fiber bundles (Beaulieu, 2011). This analysis revealed bilateral, prefrontal white matter clusters in which FA decreased in art students relative to controls over the course of the study (Fig. 3A; all *ps* FDR corrected for multiple comparisons). No other significant effects of training were found (no voxels were significant after FDR correction) when the same analysis was applied to radial diffusivity (amount of diffusion perpendicular to the principal axis), axial diffusivity (amount of diffusion parallel to the principal axis), mean diffusivity (mean amount of diffusion), or cortical gray matter thickness instead of FA.

To confirm that the clusters identified in the longitudinal FA analysis were associated with absolute decreases in FA in the art students rather than increases in FA in the control group, we calculated the mean percent change in FA within these clusters for each participant and session in both groups. However, calculating FA time courses directly from the voxels that reached significance in the longitudinal analysis would decrease the slope of the experimental group's time course and increase the slope of the control group's time course artificially due to noise-induced false positives in the whole-brain analysis. In order to prevent these false-positives from affecting the result, for each participant we calculated the mean FA percent change at each time point only in voxels that were significant in the same longitudinal GLM analysis conducted with that participant's data left out (cf. Schlegel et al., 2012). An LMM analysis of these FA change time courses revealed that art students experienced a progressive decrease in FA in bilateral prefrontal white matter (group by time interaction term $t = -2.41, p = 0.016$; Fig. 3B).

To evaluate whether a relationship existed between the visual art students' decreases in prefrontal FA and increases in creative ability, we performed correlation analyses between the FA percent change calculations and the changes in each factor score between the two administrations of the TTCT, with results shown in Fig. 4A. After FDR correction for multiple comparisons across the five factors, only changes in Factor 2 showed a significant inverse correlation with FA percent change. Therefore, decreases in FA in prefrontal white matter were associated with increases in the ability to model systems and processes creatively. Additional correlation analyses with the four TTCT submeasures that loaded highly onto Factor 2 revealed that changes in three of these – *storytelling articulateness*, *portraying movement or action*, and *emotional expressiveness* – showed an inverse relationship with changes in prefrontal white matter FA (Fig. 4B; all *ps* FDR corrected for multiple comparisons across the four submeasures). Changes in the fourth submeasure – *synthesis of figures* – showed no significant correlation with changes in prefrontal FA.

Visual perception

During each scanning session, participants completed two block-design runs in which they made judgments about two types of illusory visual stimuli. In the first "luminance" run, stimuli were based on the Craik–O'Brien–Cornsweet illusion (Fig. 1C). In this illusion, a dark-to-light gradient and a light-to-dark gradient heading in opposite directions from the center of a uniform gray rectangle cause the rectangle to appear darker on one side than the other. We introduced actual differences in the luminance between the two sides of the rectangle and asked participants to judge which side was lighter. In the second "length" run, stimuli were based on the Müller–Lyer illusion (Fig. 1D), in which a line segment with outward facing arrow ends appears longer than an identical line segment with inward facing arrow ends. We introduced actual differences in the length of the two line segments and asked participants to judge which line segment was longer. We then estimated psychometric response curves for each task, session, and

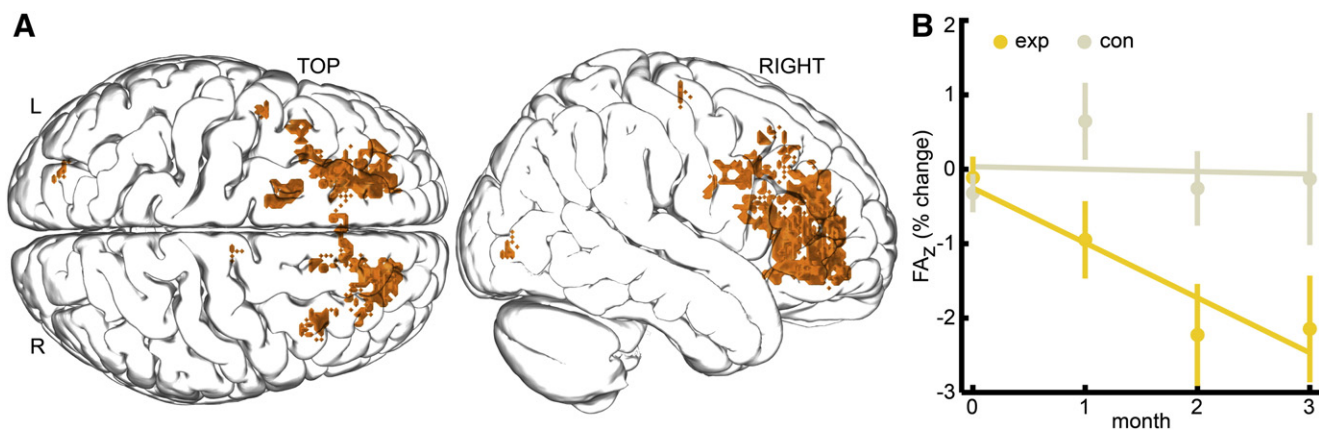


Fig. 3. Results of longitudinal analysis of white matter structure. Error bars indicate standard errors of the mean. **A.** Voxels that showed a progressive decrease in Fisher's Z transformed fractional anisotropy (FA) in art students relative to controls, shown within a glass brain in MNI space ($p \leq 0.05$, FDR corrected for multiple comparisons). All voxels are in white matter, and the majority of voxels are within the frontal lobe. **B.** Time course of FA in significant voxels from the analysis in panel A. The art students' prefrontal FA decreased progressively over the study period.

participant in order to assess a) the point of subjective equality and thus strength of the illusory effect and b) the steepness of the psychometric curve and thus the consistency of the participants' decision criteria. Using these data, we performed an LMM analysis to evaluate whether either measure changed differentially between the two groups during the study and found no effect in either measure or task (Fig. S1 & Table S4; all p s > 0.05, uncorrected). Although we found no enhancement in perceptual ability in the experimental group, we were still curious whether training would lead to differences in brain activity while making perceptual judgments. To address this question, we first performed whole-brain univariate longitudinal analyses on the BOLD measurements from each of the illusion tasks. For each task we used a permutation-based GLM with t -contrasts defined to assess group by time interactions in BOLD activity, and found no significant effects for either task (all p s > 0.05, FDR corrected for multiple comparisons). While there were no univariate BOLD differences between the groups, it is still possible that differences in more fine-grained patterns of activity arose between the groups as a result of the art students' training. To assess this possibility, we performed a whole-brain multivariate classification analysis for each session and illusion task in which we trained a linear SVM to classify between the experimental and control groups based on patterns of BOLD activity (Norman et al., 2006). If pattern level differences did arise as the art students learned, we would expect classification accuracy to increase progressively across the sessions. In order to reduce the dimensionality of the classification patterns, we used an initial voxel selection procedure to choose the 1% of voxels that showed the highest F -scores in a one-way ANOVA between the two groups' parameter estimates in a GLM contrast of task vs. rest, excluding the cross-validation holdout sample. None of these classification analyses achieved accuracies significantly above chance (one-tailed Monte Carlo test, Fig. S2 & Table S5; all p s > 0.05, uncorrected). The lack of effect in any of these analyses supports our behavioral finding that no changes occurred between the two groups in these tasks and suggests that the art training did not lead to changes in perceptual skill or strategy in the perceptual judgment tests that we used.

Perception-to-action

In each scanning session, participants also completed one block-design run in which they created 30 second gesture drawings while observing grayscale images of human figures in various poses (Fig. 1E). Each drawing was scored independently and blindly by two trained raters based on an assessment of line quality, resemblance to the observed figure, and recognizability and expressiveness of the depicted gestures. The inter-rater reliability was excellent ($\alpha = 0.82$). The

drawing ratings were averaged for each participant and session. A two-tailed, unpaired t -test found no significant difference between the two groups' drawing skills in the first session ($t(33) = 1.56$, $p = 0.128$). However, an LMM analysis performed on these mean ratings confirmed that the art students improved over time in gesture drawing ability relative to the controls (group by time interaction $t = 3.06$, $p = 0.003$; Fig. 5A).

Thus, the art students improved in both creative cognitive ability and in technical skills related to gesture drawing. To evaluate whether these two areas of improvement were related, we performed a correlation analysis between the change in TTCT CI between our two test administrations and the slope of our experimental participants' gesture drawing ability over the four neuroimaging sessions. We found no significant relationship between change in creativity and change in gesture drawing ability ($r(14) = 0.0606$, $p = 0.412$). This null finding underscores the separation between creative and technical abilities and the multifaceted nature of the training program undertaken by the art students.

Next, we asked whether the experimental group's enhancement in drawing ability tracked changes in gesture drawing related brain activity over the course of the study. To control for the possibility that differences in drawing-induced head movements between the two groups could have led to differences in BOLD measurements, we performed per-session two-tailed, unpaired t -tests on our fMRI motion correction mean relative displacement measurements. During no session was there a significant difference in head movement between the two groups (all p s > 0.05, uncorrected; Table S6). We performed whole-brain univariate longitudinal and whole-brain multivariate cross-subject classification analyses as described above for the illusion tasks. As in the illusion tasks, no significant univariate differences in brain activity developed over time between the two groups (all p s > 0.05, FDR corrected for multiple comparisons). This suggests that no mean activity differences between participant groups developed over the course of the study, as might be expected if, for instance, art students drew more vigorously as they underwent training. However, we did find that the SVM classifier in our whole-brain multivariate analysis distinguished more accurately between art students and controls based on drawing-related brain activity as the study progressed (Fig. 5B; Table S7). Initially, the classifier failed to distinguish significantly between the groups ($p = 0.249$ in a one-tailed Monte Carlo test compared to chance), but by the end of the study the classifier achieved 82.9% classification accuracy ($p = 0.002$ in the same test). To determine which areas of the brain showed patterns of activity that supported the classification between art students and controls, we visualized the voxels that were selected by our voxel selection procedure in at least 50% of classification folds (Fig. 5C). Although clusters of voxels were selected

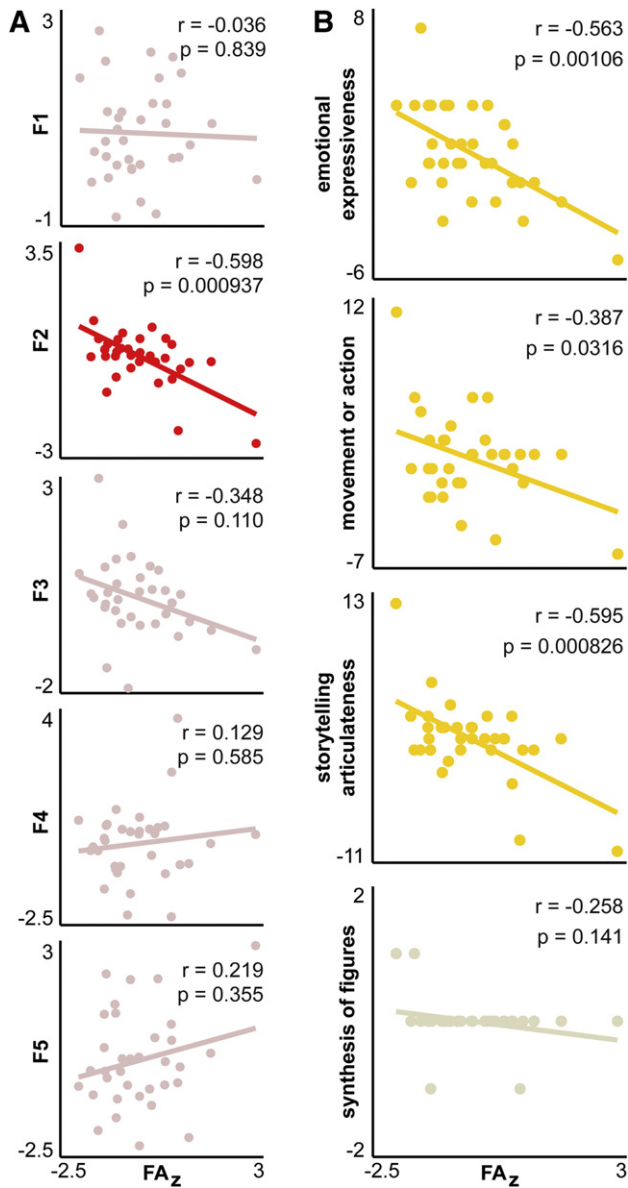


Fig. 4. Results of correlation analysis between changes in white matter organization and changes in creative thinking. A. Correlations between changes in factor scores (Fig. 2) and changes in prefrontal white matter FA (Fig. 3). Changes in Factor 2 inversely correlated with changes in prefrontal FA. All p s are FDR corrected for the five comparisons. B. Changes in three of the four TTCT submeasures that loaded highly onto Factor 2 also showed an inverse correlation with changes in prefrontal FA. All p s are FDR corrected for the four comparisons.

throughout the brain, with some clusters being chosen presumably due to noise, the largest cluster selected in each month occurred consistently in the right hemisphere of the cerebellum. Buckner et al. (2011) demonstrated previously that regions of the cerebellum overlapping with those found in the present analysis project to the hand and arm regions of left primary motor cortex and are involved in proprioceptive feedback. Miall et al. (2001) found evidence that similarly overlapping regions are responsible for coordinating eye and hand movements. Subsequent work has confirmed their findings and found that these cerebellar regions change with visuomotor task learning (Floyer-Lea and Matthews, 2004; Maquet and Schwartz, 2003). Interestingly, the selection procedure chose clusters of voxels consistently in the left motor cortex as well (see Fig. 5C). These chosen voxel clusters suggest that the classification analysis picked up on patterns of complex hand- and arm-related motor activity. To confirm that these significant classifications did not occur due to gross BOLD level differences in activity

between the groups, for each session we performed a whole-brain univariate GLM analysis to assess differences in brain activity between art students and controls. No voxels in any of these analyses reached significance (all p s > 0.05, FDR corrected for multiple comparisons). As a further control to test whether mean activity levels or fine grained spatial patterns of information were responsible for the significant classification result, we tested our classifier again, this time using the mean value of each pattern rather than the pattern itself. None of these classifications achieved accuracies significantly greater than chance (all p s > 0.05, uncorrected). Thus, fine-scale patterns of gesture drawing related neural activity in the cerebellum and cortex increasingly differentiated art students from controls during the course of the study, while overall neural activity levels remained the same. These results suggest that our participants' training in visual art entailed a reorganization of fine scale functions in these areas.

Discussion

Here we show that the brains of young adults reorganize as they learn to create visual art. Our controlled, longitudinal design involving training over three months allowed us to rule out possible confounding effects of normal aging and maturation as well as differences in motivation and initial expertise levels between the experimental and control groups. We did not find any improvements in the art students' purely perceptual skills or related brain activity relative to a control group of students who did not study art. We did, however, find that the art students improved in the ability to quickly translate observations of human figures into gesture drawings and that fine-grained patterns of drawing-related neural activity in the cerebellum and cerebral cortex increasingly differentiated the art students from the control group over the course of the study. This finding complements a recent correlational study by Chamberlain et al. (2014) showing that gray matter density in left anterior cerebellum and right medial frontal gyrus is higher in individuals who have trained in observational drawing. From their finding, it was concluded that observational drawing ability depends on differences in structural organization related to fine motor control in these areas. However, we did not find that gray matter thickness changed as a function of training in these or any other cortical areas. There are many possible interpretations of this discrepancy, among them that Chamberlain and colleagues' cross-sectional design could have found pre-existing differences in gray matter organization that determined innate potentialities for differences in drawing ability. Interestingly, the art students in our study also improved in measures of creative thinking, specifically in their ability to think divergently, model systems and processes, and use imagery. Increases in their ability to model systems and processes creatively correlated with decreases in the fractional anisotropy (FA) of prefrontal white matter. Consistent with a previous study that found creative ability to be negatively correlated with prefrontal white matter FA (Jung et al., 2010), our results suggest that changes in prefrontal white matter FA may underlie the processes by which art training leads to increased creative ability. The lack of correlation between our observed improvements in TTCT scores and gesture drawing ability supports the view that artistic training is a multifaceted process involving the development of both creative cognitive and technical skills.

Our results are also consistent with models that attribute improvements in representational artists' skills to their ability to translate perception into creative action rather than to perceive the world differently (cf. Gombrich, 1960). Like Perdreau and Cavanagh (2011), we found no special ability among artists to extract veridical properties of the physical environment through purely perceptual processes. It should be noted, however, that both our study and that of Perdreau and Cavanagh tested a specific subset of perceptual abilities; it is possible that other tests could have revealed changes in perceptual ability that our studies were unable to observe. We did, nonetheless, find that art students and non-artist controls became progressively more distinguishable via drawing-related patterns of neural activity in regions of the cerebellum and

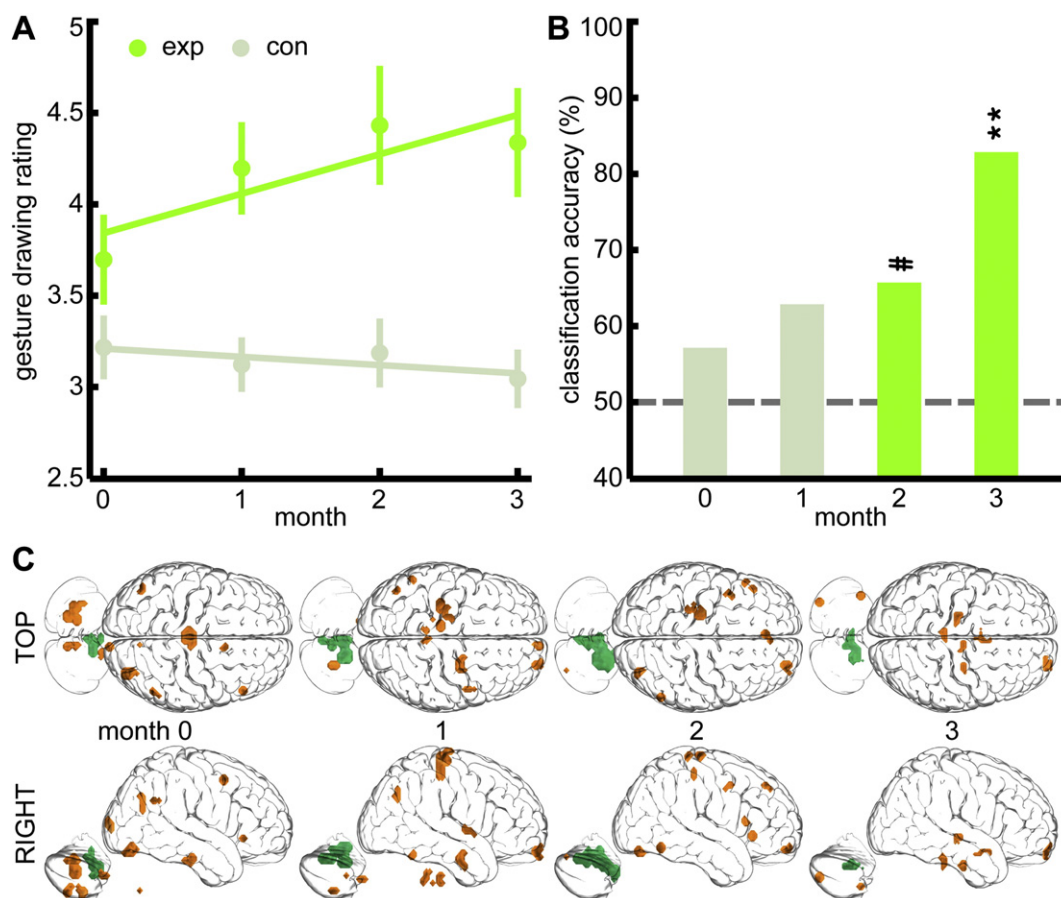


Fig. 5. Results of the gesture drawing analysis. Error bars indicate standard errors of the mean. **A.** A longitudinal LMM analysis revealed that art students improved progressively in gesture drawing ability relative to controls over the four sessions of the study. **B.** A whole-brain multivariate between-group linear SVM classification analysis based on patterns of gesture drawing-related brain activity improved progressively in its ability to distinguish art students from controls. Plot shows classification accuracy over time. Initially, the classifier could not distinguish art students from controls. By the end of the study, the classifier could distinguish between the groups with 82.9% accuracy (#: $p \leq 0.1$, **: $p \leq 0.01$). **C.** Voxels selected in each session by the analysis in panel B to be included in the classification patterns, in MNI space. Voxels are included in these plots if they were selected in at least 50% of the cross-validation folds. The largest cluster in each session is colored green. In each session, this cluster is in the area of the right anterior lobe of the cerebellum that projects to the hand and arm regions of the left motor cortex.

motor cortex that have been shown previously to mediate fine motor control, proprioceptive feedback, and coordination between eye and hand movements, and are likely involved in non-motor cognitive processes as well (Buckner, 2013; Floyer-Lea and Matthews, 2004; Maquet and Schwartz, 2003; Miall et al., 2001). Thus, our findings provide evidence that visual art training changes neural processing in regions that mediate integration between perception and action. These results are consistent with the possibility that differences in at least some representational artist's perceptual abilities may only become apparent when coupled with action, such as the skilled strokes of a paintbrush or the building up of a work of art over time through continuous comparison between what is observed and what is produced. In line with this view, Kozbelt (2001) showed that artists were better at several perceptual tasks but also that these advantages had developed largely to support drawing skills. Future research could help resolve these issues by examining explicitly the source of representational artists' increased accuracy in creating art works from observation.

The prefrontal cortex is associated with many complex behaviors that involve long-term goal making and planning (Miller et al., 2002; Tanji and Hoshi, 2001), generating novel and flexible rules (Rougier et al., 2005), and imagining future events (Addis et al., 2007), among other abilities. Common to many of these skills is the ability to represent complex processes that do not currently and may never exist in the immediate external environment (Frick et al., 2014). The prefrontal cortex therefore likely plays an important role in creative behavior and especially the creative work of an artist, which requires the flexible development of novel and

complex thoughts, processes, and objects. Indeed, Jung et al. (2010) used DTI to find that more creative individuals exhibited lower FA in prefrontal white matter tracts. However, the causal inferences that can be made from their cross-sectional design are limited. While their results are consistent with our findings, our longitudinal design provides additional evidence that creative cognition can improve with training on a time scale of three months and that prefrontal white matter reorganizes as participants become more able to think creatively.

It is worth noting that DTI measures water diffusion and so provides only an indirect measure of white matter organization. The precise microstructural correlates of FA are generally difficult to elucidate, although FA is associated with several properties of individual axons and axon bundles (Beaulieu, 2011). As creative thought often requires forming many connections between disparate concepts, one possibility for the effects we observed is that improvements in creative thinking are associated with an increase in the complexity of axonal packing (i.e. a more complex pattern of connectivity) in the frontal lobes. It is also possible that axonal demyelination played a role. Evidence has been found of experience-dependent myelination of axons in mice (Demerens et al., 1996), but a decrease in FA such as observed in the present study would be associated with decreases in axonal myelination and would require that previously unobserved learning-induced demyelination processes exist in the adult human brain. To speculate, this demyelination could occur as art students develop more efficient processing pathways (Solso, 2001) or as more creative individuals learn to avoid use of frontal inhibitory circuits. There is evidence that creative activity involves the inhibition of prefrontal activity

(Limb and Braun, 2008). Alternatively, development of the glial support network resulting from increased use of the white matter tracts we identified (e.g. to actively direct creative thought) could have led to a more complex extra-axonal environment and thus decreased FA. For instance, oligodendrocytes extend processes that wrap myelin sheaths around axons in an activity-dependent manner (Barres and Raff, 1993; Demerens et al., 1996). While increases in myelination may increase FA, extension of the orthogonally-oriented processes of oligodendrocytes might randomize water diffusion and thereby lower FA. Evidence exists that glial cells are modified by neuronal activity (Barres and Raff, 1993; Ishibashi et al., 2006), but we are not aware of direct evidence that these changes can affect FA. Future work that elucidates the cellular basis of learning-induced changes in white matter organization could shed further light on interpreting the results presented here.

How does the human brain mediate complex, creative processes such as the construction of representational works of visual art? Answers to this and related questions will not only illuminate the artistic process itself but could also lead to a more general understanding of the flexible behaviors that set humans apart as a species. An artist's work is not an innate skill and so must be developed through study and practice. The present study reveals that, at least in some cases, artistic development is a complex process involving changes in behavior along with the reorganization of both the structure and function of the brain. While we documented changes in specific aspects of creative cognition and in the integration of perception and action, future research in different artistic disciplines and among different populations will undoubtedly reveal further complexity in the creative learning process.

Acknowledgments

We thank Brenda Garand for her advice and support. This study was funded by a National Science Foundation Graduate Research Fellowship (No. 2012095475) to AS, Templeton Foundation Grant 23437 to PUT, and Dartmouth Internal Funding to MM.

AS, ER, PUT, and MM designed the study. ER taught the art courses (with other professors). AS, PA, SVF, XL, and ZL collected data. AS and SVF developed analytical tools. AS, PA, SVF, and PJK analyzed the data. All authors were involved in writing the paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2014.11.014>.

References

- Addis, D.R., Wong, A.T., Schacter, D.L., 2007. Remembering the past and imagining the future: common and distinct neural substrates during event construction and elaboration. *Neuropsychologia* 45, 1363–1377. <http://dx.doi.org/10.1016/j.neuropsychologia.2006.10.016>.
- Arden, R., Chavez, R.S., Grazioplene, R., Jung, R.E., 2010. Neuroimaging creativity: a psychometric view. *Behav. Brain Res.* 214, 143–156. <http://dx.doi.org/10.1016/j.bbr.2010.05.015>.
- Barres, B.A., Raff, M.C., 1993. Proliferation of oligodendrocyte precursor cells depends on electrical activity in axons. *Nature* 361, 258–260.
- Beaulieu, C., 2011. What makes diffusion anisotropic in the nervous system? In: Jones, D. (Ed.), *Diffusion MRI: Theory, Methods, and Applications*. Oxford University Press, New York, pp. 92–109.
- Bhattacharya, J., Petsche, H., 2005. Drawing on mind's canvas: differences in cortical integration patterns between artists and non-artists. *Hum. Brain Mapp.* 26, 1–14. <http://dx.doi.org/10.1002/hbm.20104>.
- Buckner, R.L., 2013. The cerebellum and cognitive function: 25 years of insight from anatomy and neuroimaging. *Neuron* 80, 807–815. <http://dx.doi.org/10.1016/j.neuron.2013.10.044>.
- Buckner, R.L., Krienen, F.M., Castellanos, A., Diaz, J.C., Yeo, B.T.T., 2011. The organization of the human cerebellum estimated by intrinsic functional connectivity. *J. Neurophysiol.* 106, 2322–2345. <http://dx.doi.org/10.1152/jn.00339.2011>.
- Chamberlain, R., McManus, I.C., Brunswick, N., Rankin, Q., Riley, H., Kanai, R., 2014. Drawing on the right side of the brain: a voxel-based morphometry analysis of observational drawing. *NeuroImage* 96, 167–173.

- Cohen, D.J., 2005. Look little, look often: the influence of gaze frequency on drawing accuracy. *Percept. Psychophys.* 67, 997–1009.
- Dale, A.M., Fischl, B., Sereno, M.I., 1999. Cortical surface-based analysis: I. segmentation and surface reconstruction. *NeuroImage* 9, 179–194.
- Demerens, C., Stankoff, B., Logak, M., Anglade, P., Allinquant, B., Couraud, F., Zalc, B., Lubetzki, C., 1996. Induction of myelination in the central nervous system by electrical activity. *Proc. Natl. Acad. Sci.* 93, 9887–9892.
- Dietrich, A., Kanso, R., 2010. A review of EEG, ERP, and neuroimaging studies of creativity and insight. *Psychol. Bull.* 136, 822–848. <http://dx.doi.org/10.1037/a0019749>.
- Ditye, T., Kanai, R., Bahrami, B., Muggleton, N.G., Rees, G., Walsh, V., 2013. Rapid changes in brain structure predict improvements induced by perceptual learning. *NeuroImage* 81, 205–212. <http://dx.doi.org/10.1016/j.neuroimage.2013.05.058>.
- Draganski, B., Gaser, C., Busch, V., Schuierer, G., Bogdahn, U., May, A., 2004. Changes in grey matter induced by training. *Nature* 427, 311–312.
- Driemeyer, J., Boyke, J., Gaser, C., Büchel, C., May, A., 2008. Changes in gray matter induced by learning—revisited. *PLoS One* 3, e2669. <http://dx.doi.org/10.1371/journal.pone.0002669>.
- Floyer-Lea, A., Matthews, P.M., 2004. Changing brain networks for visuomotor control with increased movement automaticity. *J. Neurophysiol.* 92, 2405–2412. <http://dx.doi.org/10.1152/jn.01092.2003>.
- Frankenstein, A., 1953. *After the Hunt: William Harnett and other American Still Life Painters 1870–1900*. University of California Press, Berkeley.
- Frick, A., Möhring, W., Newcombe, N.S., 2014. Development of mental transformation abilities. *Trends Cogn. Sci.* 1–7. <http://dx.doi.org/10.1016/j.tics.2014.05.011>.
- Fry, R.E., 1920. *Vision and Design*. Chatto & Windus, London.
- Glazek, K., 2012. Visual and motor processing in visual artists: implications for cognitive and neural mechanisms. *Psychol. Aesthet. Creat. Arts* 6, 155–167. <http://dx.doi.org/10.1037/a0025184>.
- Gombrich, E.H., 1960. *Art and Illusion: A Study in the Psychology of Pictorial Representation*. Princeton University Press, Princeton.
- Goodale, M.A., Milner, A.D., 1992. Separate visual pathways for perception and action. *Trends Neurosci.* 15, 20–25.
- Graham, D.J., Meng, M., 2011. Lightness constancy in artists. *J. Vis.* 11, 371.
- Guilford, J.P., 1967. *The Nature of Human Intelligence*. McGraw-Hill, New York.
- Hanke, M., Halchenko, Y.O., Sederberg, P.B., Hanson, S.J., Haxby, J.V., Pollmann, S., 2009. PyMVPA: a python toolbox for multivariate pattern analysis of fMRI data. *Neuroinformatics* 7, 37–53. <http://dx.doi.org/10.1007/s12021-008-9041-y>.
- Hee Kim, K., 2006. Is creativity unidimensional or multidimensional? Analyses of the Torrance tests of creative thinking. *Creat. Res. J.* 18, 251–259. http://dx.doi.org/10.1207/s15326934crj1803_2.
- Ishibashi, T., Dakin, K.A., Stevens, B., Lee, P.R., Kozlov, S.V., Stewart, C.L., Fields, R.D., 2006. Astrocytes promote myelination in response to electrical impulses. *Neuron* 49, 823–832. <http://dx.doi.org/10.1016/j.neuron.2006.02.006>.
- Jung, R.E., Grazioplene, R., Caprihan, A., Chavez, R.S., Haier, R.J., 2010. White matter integrity, creativity, and psychopathology: disentangling constructs with diffusion tensor imaging. *PLoS One* 5, e9818. <http://dx.doi.org/10.1371/journal.pone.0009818>.
- Kowatari, Y., Lee, S.H., Yamamura, H., Nagamori, Y., Levy, P., Yamane, S., Yamamoto, M., 2009. Neural networks involved in artistic creativity. *Hum. Brain Mapp.* 30, 1678–1690. <http://dx.doi.org/10.1002/hbm.20633>.
- Kozbelt, A., 2001. Artists as experts in visual cognition. *Vis. Cogn.* 8, 705–723. <http://dx.doi.org/10.1080/13506280042000090>.
- Kozbelt, A., Seeley, W.P., 2007. Integrating art historical, psychological, and neuroscientific explanations of artists' advantages in drawing and perception. *Psychol. Aesthet. Creat. Arts* 1, 80–90. <http://dx.doi.org/10.1037/1931-3896.1.2.80>.
- Limb, C.J., Braun, A.R., 2008. Neural substrates of spontaneous musical performance: an fMRI study of jazz improvisation. *PLoS One* 3, e1679. <http://dx.doi.org/10.1371/journal.pone.0001679>.
- Lövdén, M., Bodammer, N.C., Kühn, S., Kaufmann, J., Schütze, H., Tempelmann, C., Heinze, H.-J., Düzel, E., Schmiedek, F., Lindenberger, U., 2010. Experience-dependent plasticity of white-matter microstructure extends into old age. *Neuropsychologia* 48, 3878–3883. <http://dx.doi.org/10.1016/j.neuropsychologia.2010.08.026>.
- Maquet, P., Schwartz, S., 2003. Sleep-related consolidation of a visuomotor skill: brain mechanisms as assessed by functional magnetic resonance imaging. *J. Neurosci.* 23, 1432–1440.
- May, A., 2011. Experience-dependent structural plasticity in the adult human brain. *Trends Cogn. Sci.* 15, 475–482. <http://dx.doi.org/10.1016/j.tics.2011.08.002>.
- Miall, R., Reckess, G., Imamizu, H., 2001. The cerebellum coordinates eye and hand tracking movements. *Nat. Neurosci.* 4, 638–644.
- Milbrandt, M., Milbrandt, L., 2011. Creativity: what are we talking about? *Art Educ.* 8–14.
- Miller, E.K., Freedman, D.J., Wallis, J.D., 2002. The prefrontal cortex: categories, concepts and cognition. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 357, 1123–1136. <http://dx.doi.org/10.1098/rstb.2002.1099>.
- Mishkin, M., Ungerleider, L.G., 1982. Contribution of striate inputs to the visuospatial functions of parieto-preoccipital cortex in monkeys. *Behav. Brain Res.* 6, 57–77.
- Müller-Lyer, F.C., 1889. *Optische urteilstäuschungen*. *Arch. Anat. Physiol. Physiol. Abt.* 2, 263–270.
- Norman, K.A., Polyn, S.M., Detre, G.J., Haxby, J.V., 2006. Beyond mind-reading: multi-voxel pattern analysis of fMRI data. *Trends Cogn. Sci.* 10, 424–430. <http://dx.doi.org/10.1016/j.tics.2006.07.005>.
- Ostrofsky, J., Kozbelt, A., Seidel, A., 2012. Perceptual constancies and visual selection as predictors of realistic drawing skill. *Psychol. Aesthet. Creat. Arts* 6, 124–136. <http://dx.doi.org/10.1037/a0026384>.
- Perdreau, F., Cavanagh, P., 2011. Do artists see their retinas? *Front. Hum. Neurosci.* 5, 1–10. <http://dx.doi.org/10.3389/fnhum.2011.00171>.
- Perdreau, F., Cavanagh, P., 2013. The artist's advantage: better integration of object information across eye movements. *Iperception* 4, 380–395. <http://dx.doi.org/10.1068/i0574>.

- Perdreau, F., Cavanagh, P., 2014. Drawing skill is related to the efficiency of encoding object structure. *iPerception* 5, 101–119. <http://dx.doi.org/10.1068/i0635>.
- Perna, A., Tosetti, M., Montanaro, D., Morrone, M.C., 2005. Neuronal mechanisms for illusory brightness perception in humans. *Neuron* 47, 645–651. <http://dx.doi.org/10.1016/j.neuron.2005.07.012>.
- Plewan, T., Weidner, R., Eickhoff, S.B., Fink, G.R., 2012. Ventral and dorsal stream interactions during the perception of the Müller-Lyer illusion: evidence derived from fMRI and dynamic causal modeling. *J. Cogn. Neurosci.* 24, 2015–2029. http://dx.doi.org/10.1162/jocn_a_00258.
- Rougier, N.P., Noelle, D.C., Braver, T.S., Cohen, J.D., O'Reilly, R.C., 2005. Prefrontal cortex and flexible cognitive control: rules without symbols. *Proc. Natl. Acad. Sci.* 102, 7338–7343. <http://dx.doi.org/10.1073/pnas.0502455102>.
- Ruskin, J., 1857. *The Elements of Drawing*. Smith, Elder, & Company, London.
- Schlegel, A., Rudelson, J.J., Tse, P.U., 2012. White matter structure changes as adults learn a second language. *J. Cogn. Neurosci.* 24, 1664–1670. http://dx.doi.org/10.1162/jocn_a_00240.
- Scholz, J., Klein, M.C., Behrens, T.E.J., Johansen-Berg, H., 2009. Training induces changes in white-matter architecture. *Nat. Neurosci.* 12, 1370–1371. <http://dx.doi.org/10.1038/nn.2412>.
- Shiff, R., 2004. *Barnett Newman: A Catalogue Raisonné*. Yale University Press, New Haven.
- Smith, S.M., Jenkinson, M., Woolrich, M.W., Beckmann, C.F., Behrens, T.E.J., Johansen-Berg, H., Bannister, P.R., De Luca, M., Drobnjak, I., Flitney, D.E., Niazy, R.K., Saunders, J., Vickers, J., Zhang, Y., De Stefano, N., Brady, J.M., Matthews, P.M., 2004. Advances in functional and structural MR image analysis and implementation as FSL. *NeuroImage* 23 (Suppl. 1), S208–S219. <http://dx.doi.org/10.1016/j.neuroimage.2004.07.051>.
- Smith, S.M., Nichols, T.E., 2009. Threshold-free cluster enhancement: addressing problems of smoothing, threshold dependence and localisation in cluster inference. *NeuroImage* 44, 83–98. <http://dx.doi.org/10.1016/j.neuroimage.2008.03.061>.
- Solso, R.L., 2001. Brain activities in a skilled versus a novice artist: an fMRI study. *Leonardo* 34, 31–34. <http://dx.doi.org/10.1162/002409401300052479>.
- Stiles, K., Selz, P.H., 2012. *Theories and Documents of Contemporary Art: A Sourcebook of Artists' Writings*, 2nd ed. University of California Press, Berkeley.
- Tanji, J., Hoshi, E., 2001. Behavioral planning in the prefrontal cortex. *Curr. Opin. Neurobiol.* 164–170.
- Taubert, M., Draganski, B., Anwander, A., Müller, K., Horstmann, A., Villringer, A., Ragert, P., 2010. Dynamic properties of human brain structure: learning-related changes in cortical areas and associated fiber connections. *J. Neurosci.* 30, 11670–11677. <http://dx.doi.org/10.1523/JNEUROSCI.2567-10.2010>.
- Taylor, I.A., 1976. Psychological sources of creativity. *J. Creat. Behav.* 10, 193–202. <http://dx.doi.org/10.1002/j.2162-6057.1976.tb01024.x>.
- Thouless, R.H., 1932. Individual differences in phenomenal regression. *Br. J. Psychol. Gen. Sect.* 22, 216–241.
- Todorović, D., 1987. The Craik-O'Brien-Cornsweet effect: new varieties and their theoretical implications. *Percept. Psychophys.* 42, 545–560.
- Todorović, D., 2002. Constancies and illusions in visual perception. *Psihologija* 35, 125–207.
- Torrance, E.P., 1969. *Torrance Tests of Creative Thinking*. Personal Press Incorporated.