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Hemispheric Asymmetries and Individual Differences in Visual Concept Learning as Measured by Functional MRI

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Abstract

Dynamic changes in brain regions active while learning novel visual concepts were examined in humans using functional magnetic resonance imaging. Participants learned to distinguish between exemplars of two categories, formed as distortions of different unseen prototype stimuli. Regions of the right hemisphere (dorsolateral prefrontal and inferior parietal areas) were active early in learning and throughout task performance, whereas homologous portions of the left hemisphere were active only in later stages of learning. Left dorsolateral prefrontal activation was found only in participants who showed superior conceptual learning. Such a progression from initial right-hemisphere processing of specific instances to bilateral activity as left-hemisphere conceptual processes are recruited may underlie the development of many forms of visual knowledge.

Key Words: concept learning, hemispheric asymmetries, fMRI, visual learning, neural plasticity.

Much of human cognition involves interpreting a wide range of sensory inputs from the world in terms of a limited number of meaningful, abstracted categories. This interpretation occurs in recognizing objects and words and in tasks requiring special expertise such as diagnosis using X rays by radiologists and identification of enemy airplanes by military pilots [22]. For all of these domains of visual knowledge, people must learn through experience how to categorize many visual inputs into meaningful categories. Visual knowledge, therefore, involves a transition from seeing novel instances to classifying such instances into significant abstract categories. For example, in learning to recognize the letters of the alphabet, one must learn that Q, **Q**, q, Q, q, and *Q* are all instances of the letter Q, despite their physical differences.

The neural basis of such conceptual learning is unknown. Psychological studies presenting stimuli separately to the right and left hemisphere suggest, however, that the two cerebral hemispheres may play different roles in the development of categorical expertise. Studies of children learning to read or learning a language with a novel script find a right-hemisphere advantage at early stages of learning that shifts to a left-hemisphere advantage as reading becomes skilled [32, 33]. Similarly, in musical tasks, novices show a right-hemisphere advantage, whereas expert musicians show a left-hemisphere advantage [2]. These behavioral studies suggest that the right hemisphere specializes in processing specific stimuli, whereas the left hemisphere specializes in processing patterns abstracted across stimuli [13].

Consistent with this specialization for specific stimuli, behavioral research indicates that the right hemisphere performs memory judgments about specific visual items more quickly and accurately than the left hemisphere [20, 21]. The right hemisphere also is more responsive to novel stimuli than the left hemisphere [3]. Conversely, the left hemisphere performs judgments about prototypical examples of a visual concept more rapidly than the right hemisphere [19].

Behavioral studies can compare the relative speed or accuracy of entire hemispheres, but cannot elucidate the specific brain areas underlying categorization. In order to identify particular brain systems involved in conceptual learning, we studied brain activity while people learned to distinguish between two novel visual concepts using functional Magnetic Resonance Imaging (fMRI). We used a simple conceptual learning task so as to examine modulation of neural activity during the shift from novice to skilled levels of performance. Stimuli in each of two concepts were distortions of two different prototypes. Previous research has shown that visual concepts formed in this manner are learnable, and that learning is aided by feedback and low levels of distortion from the prototype [10, 24]. These conditions were employed in order to monitor changes in patterns of brain activation that occurred in a single imaging session as people acquired novel visual concepts. The transition from right-hemisphere dominant naive performance to left-hemisphere dominant skilled performance can occur within a single session, as seen in musical [16, 36] and visuospatial [17] domains.

Method

Participants

Ten adults (7 men, 3 women; mean age 29) participated in this study. All participants were right handed, spoke fluent English, and had no neurological disorders. Participants gave informed consent using a form approved by the Stanford University Institutional Review Board.

Materials

The prototype stimuli were taken from Fried and Holyoak [10, Experiment 1], and are shown in Figure 1. Each prototype was a pattern of red and blue boxes in a 10 x 10 checkerboard grid. Concept exemplars were formed by changing the color of each square with a 7% probability (considered a low level of distortion by Fried and Holyoak). Two lists of 48 exemplars were formed; each list had 24 Smith and 24 Jones stimuli, randomly ordered with the constraint that there were 6 Smith and 6 Jones stimuli in each quarter of the list. No stimulus was repeated within or across lists.

Procedure

Participants were instructed that they would be learning to distinguish between the paintings of two modern artists, Smith and Jones. For each painting they were to decide which artist had painted it, and would be given feedback. They were told that at first they would have to guess, but that eventually they would know how to classify the items. The participants did not view any exemplars before scanning.

Each participant completed two scans, with a brief (approximately 2 minute) break between scans. The stimulus lists were counterbalanced for use in scans 1 and 2 across participants. During the scans, stimuli were presented for 2500 ms, during which participants responded by pressing optical switches. There were separate switches for Smith and Jones held in different hands. After the stimulus disappeared, feedback (the single word "Smith" or "Jones") appeared for 500 ms. There was an intertrial interval of 500 ms. Blocks of 12 classification trials alternated with blocks of 12 baseline task trials, for a total of 4 blocks of each in each scan. Thus across both scans there was a total of 96 categorization trials; these were broken into quartiles (4 groups of 24) for purposes of analysis. In baseline trials, participants were shown the baseline stimulus (a regular checkerboard, Figure 1) and randomly pressed one of the two response keys. In the place of feedback, the word "Board" was presented.

fMRI Methods

Imaging was performed with a 1.5 T whole-body MRI scanner (GE Medical Systems Signa). A prototype receive-only whole-head coil was used for signal reception. A bite bar formed with each participant's dental impression was used to minimize head motion.

Stimuli were visually presented by back-projecting the images, via a magnet-compatible projector, onto a screen located above the participant's neck. Images were viewed from a mirror mounted above the participant's head. Sixteen contiguous 4 mm thick slices were acquired parallel to the anterior commisure (AC) - posterior commisure (PC) plane, extending from 16 mm below to 44 mm above the (AC) - (PC) plane. Thus, there was incomplete coverage of inferior portions of the cerebellum and temporal lobe, and superior portions of the parietal and frontal lobes. T1-weighted flow compensated spin-warp anatomy images were acquired for each of the slices imaged in the functional scans. A T2*-sensitive gradient echo 3D spiral pulse sequence was used for functional imaging with parameters of TE = 40 ms, TR = 1080 ms, flip angle = 22, 4 interleaves, and inplane resolution = 2.35 x 2.35 mm. The interscan interval was 4.32 s.

FMRI data were analyzed for activation related to the concept learning task using the general linear model and the theory of Gaussian fields. Image reconstruction was performed off-line. Functional images were motion corrected using an automated registration algorithm (AIR 3.0, [42]). Images were normalized to a standard space [38] using an 8 parameter linear transformation implemented in SPM 96 (Welcome Department of Cognitive Neurology, London, UK). Normalized images were smoothed via SPM, using a 6.0 mm Gaussian kernel. The fMRI statistics program of SPM 96 was used to estimate the effects of condition at each voxel according to the general linear model [11]. The analysis was entered as an epoch design of the fixed response / box car form. The design matrix included global signal intensity as a confounding covariate and this analysis can therefore be regarded as an ANCOVA. No temporal derivative and no additional confounding variables were entered. A high pass filter with a cut-off period of 120 s was used. Linear contrasts were used to test hypotheses about regionally specific effects, forming a statistical parametric map of voxel values for each contrast. These maps were transformed to the unit normal distribution and thresholded at p = .001 (uncorrected).

Distributional approximations from the theory of Gaussian fields were used to characterize the statistical significance of activation maps in terms of the probability that an observed peak height or region size could have occurred by chance across the entire imaged volume [12].

Results

Behavioral Results

Accuracy of classification was calculated for each participant across quartiles of 24 classification trials each. A one-way ANOVA indicated that participants improved their classification across quartiles, $F(3, 27) = 8.5$, $p < .001$. Performance improved from the first ($M = 64$ %) to the second ($M = 82$ %; $t(9) = 3.92$, $p < .005$) quartile, but remained constant in the third ($M = 79$ %), and fourth ($M = 79$ %) quartiles.

There were robust individual differences in classification performance (Figure 3a). Six participants mastered the classification task, reaching a mean final quartile classification score of 91%. Four participants, however, showed little or no learning; their mean final quartile classification score was 61%. The cut – off between learners and nonlearners was set at 83 % (20 out of 24 correct responses) in the final quartile; learners ranged between 88 % and 100 % on the final quartile, whereas nonlearners ranged between 50 % and 75 %. A two-way ANOVA with factors of group (learners and nonlearners) and quartile found a main effect of group, such that learners performed better than nonlearners, $F(1, 8) = 11.5$, $p < .01$, and an interaction of group and quartile, such that the difference between learners and nonlearners increased across quartiles, $F(3, 24) = 3.59$, $p < .05$. Nonlearners did not show improved performance across blocks: the simple effect of quartile for nonlearners was not significant, $F < 1.0$. Previous categorization learning research has found individual differences in learning [1, 6], but the reasons for these differences are not well understood.

Response time decreased across quartiles for both learners and nonlearners. A two-way ANOVA with factors of quartile and group (learners, nonlearners) found a significant effect of quartile, $F(3, 24) = 6.98$, $p < .005$, but no effect of group and no interaction.

Classification > Baseline Activations

Areas of greater activity during classification than baseline across trials are shown in Table 1a. There was prominent activation of right dorsolateral prefrontal and bilateral parietal regions, areas associated with reasoning and working memory. In addition, activation was found in the bilateral middle occipital cortices, bilateral inferior frontal areas, and the anterior cingulate.

Learning-Related Changes in Activity

Changes in activity in frontal and parietal brain areas were found across the four quartiles of visual concept learning (Figure 2). In the first quartile, classification performance was poor across participants. Activation in the classification task relative to the baseline task was limited to right-hemisphere areas of the frontal and parietal lobes. Beginning in the second quartile, a high level of classification ability was attained, and left hemisphere activation was present in addition to right-hemisphere activation. Left parietal activation was present in the second through fourth quartiles. A linear contrast in SPM showed a significant increase in left parietal activation across quartiles. Left dorsolateral prefrontal activation was present in quartiles 2 and 3, and was present but did not reach the threshold of significance in quartile 4, which is probably due to insufficient power attributable to the low numbers of participants. The right frontal and parietal activity did not increase significantly across quartiles.

In addition to frontal and parietal areas, activation in both right and left occipital gyri increased across quartiles. A two-way ANOVA with factors of quartile and hemisphere (left, right) found a main effect of quartile, $F(3, 48) = 3.5$, $p < .05$, but no main effect of hemisphere or interaction. The dependent measure was the mean signal change at the cluster of 125 pixels extending in three dimensions (8 x 8 x 16 mm) from the coordinates of the maximum Z score (as given in Table 1).

Individual Differences

The performance differences in classification between learners and nonlearners were associated with one reliable brain activation difference. The fMRI statistics program (using parameters as described in Procedure), was used to perform an interaction analysis of brain activation during categorization relative to baseline across averaged volumes for learners and nonlearners. The left prefrontal cortex *(x = -54, y = 30, z = 24; BA 9/46;* Figure 3b) was significantly more active for learners than nonlearners. As shown in Figure 3, activation in the left prefrontal cortex for learners increased across quartiles, but activation in nonlearners remained constant across quartiles.

Baseline > Classification Activations

Areas listed in Table 1b were less active during classification than during the baseline task: the bilateral superior temporal gyri, superior and medial frontal areas, and posterior cingulate and precuneus. The superior frontal deactivation decreased across quartiles, whereas the precuneus / posterior cingulate deactivation increased across quartiles.

Discussion

The results presented here delineate a dynamic network of neural systems underlying visual concept acquisition. In the initial, naive stage of learning, stimuli could only be processed as specific visual patterns, and right-hemisphere areas were active, including right prefrontal and inferior parietal. As learning progressed, the left parietal area was recruited. Left prefrontal activation was found only in participants with highly developed conceptual knowledge.

Several visual reasoning tasks have found a combination of right prefrontal and bilateral parietal brain activity. In one study, participants had to decide which pattern would complete a sequence on the basis of visual features [26]. In another, participants classified pictures of animals on the basis of a previously learned verbal rule [35]. In the present study, participants formed rules to differentiate between novel visual patterns, then implemented these rules. In all of the tasks, participants were required to analyze the features of a visual stimulus, decide on a rule that applies to these features, and make a decision on the basis of this rule. Thus, there is convergent evidence that right prefrontal and bilateral parietal areas are involved in visual reasoning. Furthermore, these areas have also been shown to be active in visuospatial working memory tasks [14, 34]. The consistency of right hemisphere (both frontal and parietal) activity during learning implies that the right hemisphere plays a role in stimulus processing (such as visual working memory, or feature analysis) that is independent of learning. The left parietal activity increased across quartiles, indicating a learning related change, but was not significantly more active in learners than in nonlearners. It remains a task for future research to clarify the role that the left parietal area is playing in classification.

Left dorsolateral frontal activity was found only in participants who showed high levels of classification learning. This finding is consistent with research that finds left frontal activation in analytic problem solving tasks [25, 26], in working memory tasks with verbal and analytic elements [34], and participation of left hemisphere areas in formal, content-independent, reasoning [41]. The presence of left frontal activation as a marker for classification learning indicates that analytic reasoning may be involved in induction of pattern knowledge. Thus, left frontal areas may play a crucial role in gaining expertise in classification.

What role might the left dorsolateral frontal activation be playing in categorization? One possibility is that it may reflect verbal rule formation. Typically, participants who perform well on this task report noticing and utilizing rules about the presence of particular visual features (e.g., a staircase -like appearance). Another possibility is that it reflects other abstraction processes. There is much controversy in the concept learning literature revolving around whether participants perform abstraction at the point of learning (storing information about the prototypical pattern), or whether participants store individual concept exemplars and perform abstraction at test by computing the similarity of the test stimulus to the previously learned exemplars [6]. The present results do not provide evidence for deciding between either possible representation of conceptual knowledge. The left inferior frontal activation could be indicative of either forming and applying an abstract representation, or could reflect the exemplar comparison and decision making process.

It should be noted that the concept learned by participants in the present study was relatively simple, and most participants achieved high degrees of classification accuracy in few trials. However, due to the short training period participants did not achieve an “automatic” or “overlearned” level of performance. It remains a topic for future research to explore the neural changes underlying classification expertise after extended training.

In addition to parietal and dorsolateral frontal areas, greater activation was found in the bilateral inferior frontal lobes, anterior cingulate, and bilateral occipital lobes during classification than during baseline. The bilateral occipital lobe activation increased across quartiles, whereas the other activations remained constant. Bilateral inferior frontal activity in the area of the frontal operculum is often found in working memory tasks and is associated with maintenance of information [5]; left opercular activity in particular is associated with verbal rehearsal [9, 34]. The anterior cingulate is active in a wide variety of tasks, and may reflect attentional factors related to online monitoring of task performance [4, 9, 27].

The bilateral occipital lobe activation, which increased across quartiles, may be related to visual feature analysis in the extrastriate cortex. In a study of concept learning using dot pattern stimuli, Reber, Stark, and Squire [28, 29] found greater occipital activation for exemplars than for random stimuli when participants made recognition decisions, but less activation for exemplars than random stimuli when participants judged whether stimuli were category members. These results, taken together, indicate that occipital lobe activation can be altered dynamically depending on task demands. It is unclear why category membership judgment led to greater activation than baseline in the present study, but lower activation than baseline in the Reber et al. studies and the present study. The key may be the difference between the baseline tasks in the two studies. In the present study, subjects always saw the same stimulus and made the same response in the baseline condition, and thus the baseline task required very little feature analysis. In the Reber et al. study participants saw novel random stimuli, with novel features, which may have required more feature analysis than the familiar exemplars.

Several areas were less active during classification than during the baseline task: the bilateral superior temporal gyri, superior and medial frontal areas, and posterior cingulate and precuneus. Due to the relatively simple nature of the baseline task, it is reasonable to interpret these activations as areas that are deactivated during the classification task. Deactivation in areas related to audition such as the superior temporal gyri may reflect a suppression of auditory attention during a demanding visual task [31]. The left superior temporal gyrus deactivation increased across quartiles, but not the right superior temporal, indicating greater suppression in left auditory areas as learning occurred. The bilateral frontal pole and medial frontal cortices, and posterior cingulate and precuneus commonly show lessened activation in more difficult cognitive tasks relative to baseline tasks. These deactivations may reflect attention or extraneous thought processes during the relatively unconstrained baseline task [30]. The superior frontal deactivation decreased across quartiles, whereas the precuneus / posterior cingulate deactivation increased across quartiles; it is unknown why these areas should change over trials, and why they should change in opposite directions.

The neuroimaging literature suggests several types of learning-related changes, or neural plasticity, underlying learning. The present study found a brain activation associated with successful learning: high levels of classification learning were found only in participants who also showed left frontal activation. Other studies find other patterns of learning-related changes. In motor learning, Karni et al. [15] found increased activation in primary motor cortex for a learned finger tapping sequence. Conversely, priming studies find a relative decrease in activation for repeated items relative to novel items. Conceptual priming tasks involve decreases in left inferior frontal cortex involved with conceptual processing [8, 27] whereas perceptual priming tasks involve decreases in occipital cortex involved in visual processing [37]. In addition to local increases or decreases in brain activation, shifts between brain areas have been found. During learning to read mirror reversed text there is a shift in activation from right dorsal visuospatial processing areas to left ventral visual processing areas [23]. Thus, different types of learning are associated with different patterns of neural change.

The present findings provide a new perspective on parallel processing in the right and left hemispheres. There is a considerable literature indicating that, for well-known information, the right hemisphere analyzes stimuli in terms of specific or metric properties, whereas the left hemisphere analyzes stimuli in terms of abstracted categories. For example, identical stimuli yield a right-hemisphere advantage when requiring a metric or coordinate analysis, but a left-hemisphere advantage when requiring a categorical analysis [17]. Commissurotomy patients analyze identical stimuli based on visual form in the right hemisphere, but based on conceptual associations in the left hemisphere [18]. Patients with right-hemisphere lesions have difficulty identifying objects presented in unusual views or shadows, where identification depends upon access to a canonical or abstract view [7, 39, 40]. In contrast, patients with left-hemisphere lesions have difficulty matching exemplars that have the same abstract meaning but differ in visual details [7, 40].

In the present study, the right-hemisphere frontal and parietal activations were present from the beginning and persisted throughout learning. They did not differ reliably in learners and nonlearners. Thus, the right-hemisphere activations appear to be related to constant processes of visuospatial analysis of stimulus specifics that are dissociable from categorical learning. Indeed, such right-hemisphere processes would have to be insulated from categorical knowledge in order to maintain their focus on stimulus-specific properties, and it is to be expected that this focus would be maintained across the task. Left-hemisphere activation occurred as participants learned abstract categories applicable to the specific stimuli; the left-frontal activations differed as a function of successful category learning. Thus, the left hemisphere demonstrated category-learning plasticity through experience. The rapid educability of the left hemisphere would be useful in allowing people to quickly learn and apply new abstract categories. This study, therefore, reveals a pattern of a stable right-hemisphere system for analysis of visual specifics and a dynamic left-hemisphere system for learning visual categories. Such parallel processes in the cerebral hemispheres provide for a powerful combination of continuity and adaptive change in visual knowledge.

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Table 1a: Classification > Baseline Activations

Region	BA	k	Z	x	y	z	Change
Right prefrontal	9, 46	1690	7.3	48	38	32	=
Left inferior frontal	45, 47	709	5.9	-34	24	0	=
Right inferior frontal	45, 47	661	7.6	34	30	0	=
Left inferior parietal	7	1619	6.2	-26	-74	48	+
Right inferior parietal	7	1998	6.9	20	-74	44	=
Left middle occipital	18	678	6.5	-32	-88	12	+
Right middle occipital	18	806	6.3	32	-80	32	+
Anterior cingulate	32	298	5.0	2	36	40	=

Table 1b: Baseline > Classification Activations

Region	BA	k	Z	x	y	z	Change
Bilateral superior, medial frontal	10, 11	3041	7.9	-4	64	-12	-
Bilateral post. cingulate, precuneus	31, 18	1417	6.7	-8	-52	28	+
Right superior temporal	22	2874	6.6	70	-28	0	=
Left superior temporal	22	4452	6.5	-48	-20	4	+

Note: All areas had a corrected conjoint height and extent probability of $p < .05$. BA: Broadman's area. k: number of voxels. Z: maximum z score. x, y, z: Tailarach coordinates of the maximum z score. Change: direction of change across quartiles. +: increase. -: decrease. =: no change.

Figure Captions

Figure 1 a: Concept prototype and sample stimuli for the two concepts used in the study. Stimuli were formed by randomly reversing the color of 7% of the square elements. b: Regular checkerboard stimulus used in baseline trials.

Figure 2. Areas of activation across quartiles for all participants; each quartile consisted of two blocks of 12 classification trials, and compromised half of a scan.

Figure 3 a: Percentage correct on the classification task across quartiles for learners and non learners. b: Areas of differential activation in learners and nonlearners. c: Percentage change in fMRI signal between categorization and baseline tasks in learners and nonlearners for a pixel cluster in the left dorsolateral prefrontal area. The cluster was centered at (x = -54, y = 30, z = 24) and included 125 pixels extending in three dimensions (8 x 8 x 16 mm) from the center coordinate.