Global topological dominance in the left hemisphere

Bo Wang*, Tian Gang Zhou, Yan Zhuo*, and Lin Chen

State Key Laboratory of Brain and Cognitive Science, Institute of Biophysics, Chinese Academy of Sciences, 15 Datun Road, 100101 Beijing, China

Communicated by Robert Desimone, Massachusetts Institute of Technology, Cambridge, MA, October 17, 2007 (received for review August 9, 2007)

A series of experiments with right-handers demonstrated that the left hemisphere (LH) is reliably and consistently superior to the right hemisphere (RH) for global topological perception. These experiments generalized the topological account of lateralization to different kinds of topological properties (including holes, inside/outside relation, and "presence vs. absence") in comparison with a broad spectrum of geometric properties, including orientation, distance, size, mirror-symmetry, parallelism, collinearity, etc. The stimuli and paradigms used were also designed to prevent subjects from using various nontopological properties in performing the tasks of topological discrimination. Furthermore, task factors commonly considered in the study of hemispheric asymmetry, such as response latency vs. accuracy, vertical vs. horizontal presentation, detection vs. recognition, and simultaneous vs. sequential judgment, were manipulated to not be confounding factors. Moreover, left-handed subjects were tested and showed the right lateralization of topological perception, in the opposite direction of lateralization compared with right-handers. In addition, the functional magnetic resonance imaging measure revealed that only a region in the left temporal gyrus was consistently more activated across subjects in the task of topological discrimination, consistent with the behavioral results. In summary, the global topological dominance in the LH is well supported by the converging evidence from the variety of paradigms and techniques, and it suggests a unified solution to the current major controversies on visual lateralization.

visual lateralization | perception | temporal gyrus | holes | inside/outside relation

Hemispheric asymmetry, namely the specialization of the right and left hemispheres (RH and LH) for cognitive functions, has been widely recognized. Yet, despite efforts for well over a century, there does not seem to be a consensus about how to characterize the hemispheric specialization in a unified manner (1). For instance, on the whole, evidence for lateralization in low-level visual functions remains inconsistent (1), as exemplified in the popular "whole vs. part" analysis of visual hemispheric specialization (2, 3).

The whole vs. part relationship has been a central concern in various theories on visual perception, including those on hemispheric specialization. The "global precedence" hypothesis (4) refers to the finding that subjects responded faster to a compound letter relative to its component letters, and the compound letter interfered with responses to the component letters when the two levels were incompatible, but not vice versa. Behavioral studies have documented a RH-whole/LH-part asymmetry (5). For example, reaction times (RTs) to compound forms presented in the left visual field (LVF) were found to be shorter than those for the right visual field (RVF), and a reverse pattern was found for RTs to component forms (5). However, even though these findings were often taken as evidence for holistic processing in the RH, the asymmetry is weak, unreliable, and controversial (6).

Neuroimaging studies have found conflicting results as well. For example, some PET studies found that attention to compound letters enhanced activation over the right lingual gyrus, whereas attention to component letters did so over the left inferior occipital cortex (7). A functional MRI (fMRI) study found similar hemispheric asymmetry in whole–part processing over the occipitotemporal cortical junctions (8). However, other studies failed to replicate such RH-whole/LH-part asymmetry (9).

Why are these lateralization results so inconsistent and controversial? We believe that hemispheric specialization is part of the overall brain function; understanding what is being lateralized is critically dependent on our conceptualization of what the brain does (10). In particular, understanding visual hemispheric specialization from the perspective of the "global vs. local" relationship depends on how we answer the fundamental question of "What are the primitives of visual perception" (11, 12) and, accordingly, how we define precisely, with psychological reality, the concepts of "global" and "local" (11).

The literature on the global precedence hypothesis tends to confuse the whole vs. part or the "compound vs. component" with the global vs. local. However, it is not difficult to see that "whole (or compound) precedence" would not always be valid, because no claim could be safely made that a whole (e.g., a forest) is before its parts (e.g., a tree) in perception. It obviously depends on viewing conditions. In general, the hierarchical structure of a whole object being composed of its parts, although a natural aspect of the structure of the physical world, may not be a proper way to define the global vs. local relation, grounded in psychological reality (11).

The topological approach to perceptual organization (11, 13–15) provides a new definition of global vs. local and a new perspective in viewing the global vs. local relation. One important factor in evaluating potential primitives for visual representation is their relative stability under changes. From the perspective of the topological approach, global is linked to invariance or stability preserved under transformations. A property is considered more global (or stable) the more general the transformation group is, under which this property remains invariant. Among other form properties, topological properties, such as holes, are structurally most stable under transformations; i.e., topological transformations, which intuitively can be imagined as a smooth "rubber-sheet" distortion, cannot create or destroy holes, whereas they alter other geometrical properties. The topological properties, therefore, are considered the most global. Given the present definition of global and local, global precedence can be stated in a precise way, that is, the claim at the core of the "global-first" topological approach that global topological perception is before perception of local featural properties (11).

The present study applied the global-first topological approach to investigate the visual lateralization, with a total of eight behavioral experiments plus two fMRI conditions.

Results

We measured the hemispheric specialization for topological discrimination, applying the paradigm of "configural superiority

Author contributions: B.W., Y.Z., and L.C. designed research; B.W. performed research; T.G.Z. and Y.Z. contributed new reagents/analytic tools; B.W., T.G.Z., and Y.Z. analyzed data; and B.W., Y.Z., and L.C. wrote the paper.

The authors declare no conflict of interest.

*To whom correspondence may be addressed. E-mail: bwang@cogsci.ibp.ac.cn or yzhuo@cogsci.ibp.ac.cn.

This article contains supporting information online at www.pnas.org/cgi/content/full/0709664104/DC1.

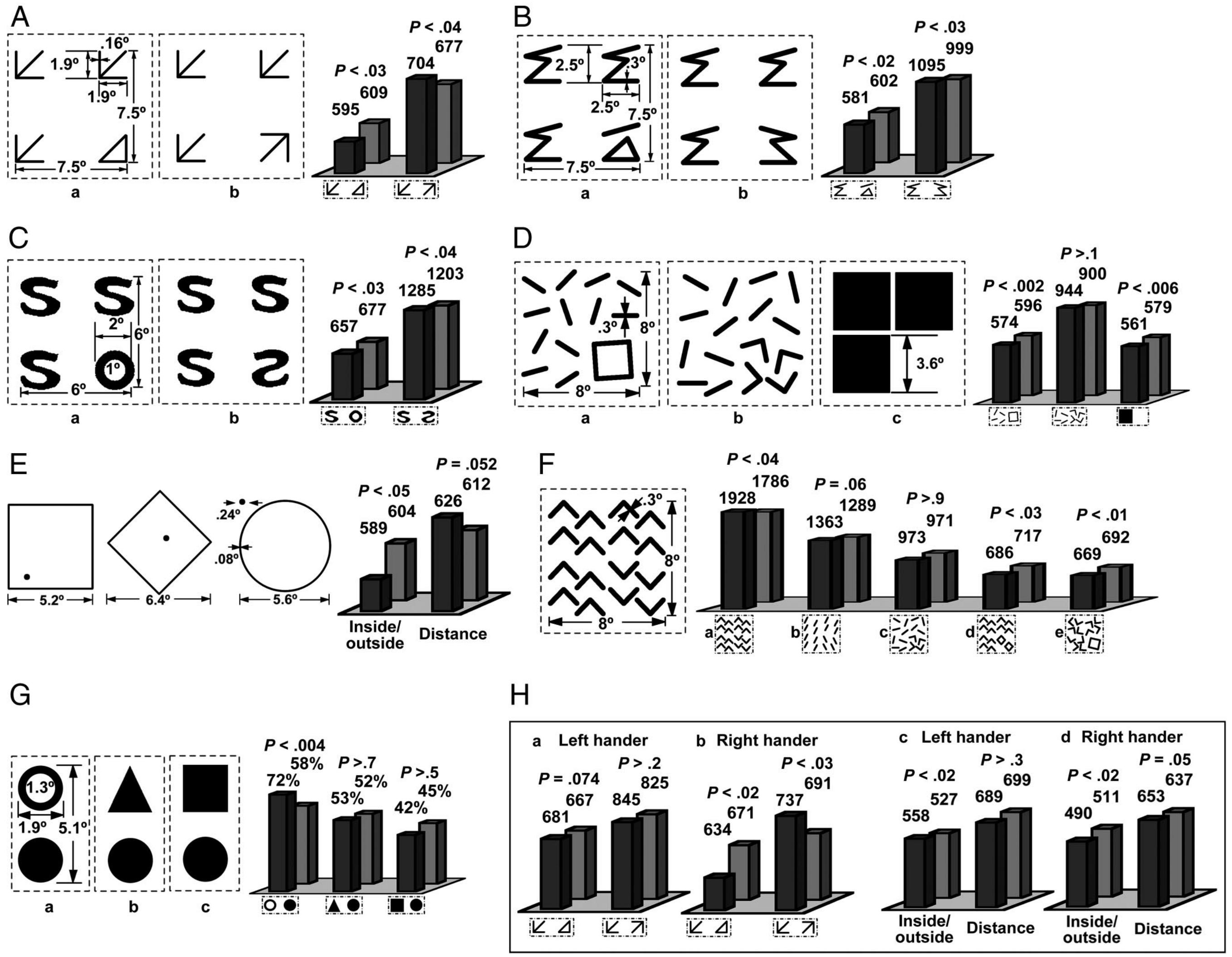

Fig. 1. (*A–H*) Schematic depiction of stimuli and results of experiments 1–8. Dark and light gray bars depict results from RVF and LVF presentations, respectively. Numbers and percentages show RTs in ms and correct response rates, respectively. All *P* values are from pairwise *t* tests for significant difference in RT or accuracy between corresponding RVF and LVF presentations.

effects" (16), which refer to the findings that configural relations between simple components rather than the components themselves may play a basic role in visual processing. Configural effects were originally revealed by an odd quadrant task, in which subjects were asked to report which quadrant differs from the other three, as illustrated in Fig. 1*A*. This odd quadrant task was adapted in our divided-visual-field experiments. Subjects in experiments 1–7 were all strongly right-handed.

LH-Hole/RH-Orientation Asymmetry. Experiment 1 measured lateralization based on the topological difference in closure (or holes), by using the stimulus of "triangle–arrow pair" (11, 16) shown in Fig. 1*Aa*. The triangle in the odd quadrant was made up of exactly the same three line segments as the arrows in the rest of the quadrants, but its closed nature makes it topologically different from the arrows. The stimulus illustrated in Fig. 1*Ab* served as a discrimination task based on orientation of arrows. As shown in Fig. 1*A*, the topological discrimination based on closure was superior in the LH than in the RH: The triangle–arrow pair trials were evaluated faster when they were presented in the RVF (initially to the LH) than they were when presented in the LVF (initially to the RH), whereas a RH advantage for an orientation task was found [the interaction of the task (a between-subjects factor) and hemisphere: $F_{(1,30)} = 12.84$, $P < 0.002$].

LH-Hole/RH-Mirror-Symmetry Asymmetry, Controlling for Terminators. Even though the triangle–arrow pair is well controlled for various local features, the topological account may still be challenged by the counterexplanation: The LH superiority is due to a difference not in closure but in the number of terminators (17). Experiment 2 adopted a pair of stimuli (Fig. 1*Ba*) to address the terminator issue. The stimuli possess exactly the same four line segments and, particularly, the same number (two) of terminators, but they differ in topology of both closure and connectivity (Fig. 1*Ba*). Another pair of stimuli (Fig. 1*Bb*) was used for a discrimination task based on mirror-symmetry. The procedure used in experiment 2 (and in the experiments 3, 4, and 6) is the same as that used in experiment 1 except that subjects were asked to report which quadrant was different from the rest. The results still showed the LH advantage for the topological discrimination (Fig. 1*B*). The RTs for the stimuli shown in Fig. 1*Ba* were faster when stimuli were presented in the RVF than they were when presented in the LVF; in contrast, the lateralization of mirror-symmetry was reversed [the interaction of task and hemisphere: $F_{(1,13)} = 9.21$, $P < 0.01$].

LH-Hole Superiority, Generalized to 2D Forms. No 1D figures can be actually drawn; rather, all drawn figures are 2D. The concept of "closure" addressed in experiments 1 and 2 is, therefore, the concept of "hole" in 2D forms (11). Particularly, the notion of a terminator, namely the end of a line segment, is essentially 1D and not well defined with respect to 2D figures. For instance, should one consider a solid square to possess two, four, or zero terminators, and a disk to possess zero or infinite number of terminators? Using 2D forms in testing for the topological account would, therefore, leave no room for any arguments based on terminator.

In experiment 3, generalizing the topological account to 2D forms, we used 2D figures (a ring and an S-shaped figure, hereafter referred to as **S**) as stimuli (Fig. 1*Ca*), which were different with respect to holes (11). The **S** was also specifically designed to have its area set to approximate the area of the ring and to make its shape irregular to eliminate possible effects of subjective contours or other organization factors. The **S**, together with its mirror image, was also used to construct a mirror-symmetry task (Fig. 1*Cb*). Again, we found the LH superiority for the discrimination based on holes (Fig. 1*C*): The RT for discriminating the **S** from the ring was faster when they were initially presented in the RVF than when presented in the LVF, and like in experiment 2, we also found the RH advantage for the discrimination of mirror-symmetry [the interaction of task and hemisphere: $F_{(1,12)} = 7.82$, $P < 0.02$].

LH-Topology Superiority, Generalized to Presence vs. Absence. Three stimuli used in experiment 4 were adapted from refs. 11 and 16 (Fig. 1*D*). In Fig. 1*Da*, the odd quadrant contained a hollow square (a hole), in comparison with four bars randomly distributed in each of the remaining quadrants. Fig. 1*Db* represents a task based on collinearity. Fig. 1*Dc* was designed in such a way that the odd quadrant contains no figure, whereas the remaining quadrants each contain a large solid square. One can hardly imagine a task easier than this odd quadrant task; therefore, it should be used to establish a baseline for the easiest task. Moreover, the topological approach leads to a novel analysis of the nature of the baseline: The property of presence vs. absence may also be considered a kind of topological invariant, because topological transformations neither create nor destroy objects. Hence, despite their great difference in local features, Fig. 1 *Da* and *Dc* share the same intrinsic characteristic of topological difference. Whereas the previous three experiments tested with one kind of topological property, namely holes, experiment 4 tested for generalization to two kinds of topological properties, holes and presence vs. absence, in comparison with collinearity.

As shown in Fig. 1*D*, there is no significant difference in RTs between the hole task and the baseline task. For the primary interest of this study, both of these two tasks demonstrate the LH superiority for topological discrimination, and there is no significant difference between them in the degree of RVF advantage (the RT with RVF – the RT with LVF) [−22 vs. −17 ms; $F_{(1,11)} = 0.55$, $P > 0.4$]; in contrast, no significant lateralization was found for the collinearity task [the interaction of task and hemisphere: $F_{(2,22)} = 5.92$, $P < 0.03$].

LH-Topology Superiority, Generalized to Inside/Outside Relation. In addition to the two kinds of topological properties tested in experiments 1–4, there is yet another kind of topological invariant, the inside/outside relation (Fig. 1*E*).

In experiment 5, we further tested the LH superiority for inside/outside relation, in comparison with detection of distance. The stimuli (Fig. 1*E*) for the inside/outside task and the distance task are actually the same: A dot may be located inside or outside a hollow square, ring, or diamond, and at different distances from the nearest edges of these hollow figures. However, in the inside/outside task, subjects were asked to report whether a dot was located inside or outside a hollow figure; in contrast, in the distance task, a dot was closer to or farther from the nearest edge of a hollow figure. The LH superiority for topological perception was found again (Fig. 1*E*); in contrast, the distance task, like tasks for other local features, showed an RH advantage [the interaction of task (as a between-subjects factor) and hemisphere: $F_{(1,34)} = 8.88$, $P < 0.006$].

LH-Topology Superiority, in Comparison with Different Levels of Geometries. In experiment 6, using five stimuli (Fig. 1*F*), we further systematically measured the changing pattern of lateralization as one varies form properties at different levels of geometries: In turn, the differences in orientation of angles (a kind of Euclidean property) (Fig. 1*Fa*), parallelism (a kind of affine property) (Fig. 1*Fb*), collinearity (a kind of projective property) (Fig. 1*Fc*), and holes (Fig. 1 *Fd* and *Fe*). These constitute a hierarchy of geometries according to Klein's Erlangen Program, which provides a formal way to stratify geometrical properties with respect to their structural stability (part IV in ref. 11). Previous tests found that the relative salience of different geometric properties is remarkably consistent with this hierarchy of geometries (11, 14).

The results (Fig. 1*F*) replicated a clear-cut correlation between the order of RTs and the different levels of geometries stratified in an ascending order of stability, and, particularly, they showed a consistent pattern of hemispheric specialization: LH is superior for the topological perception in both Fig. 1 *Fd* and *Fe*, in comparison with a wide spectrum of local geometric properties, which were either lateralized in the RH or showed no lateralization [the interaction of task and hemisphere: $F_{(4,60)} = 4.79$, $P < 0.03$].

Response Accuracy also Revealed LH-Topology Superiority. All previous six experiments used RT as an index to measure lateralization. In experiment 7, we adopted sensitivity measurement as another index. The three pairs of stimuli (Fig. 1*G*), adapted from ref. 13, originally revealed the visual sensitivity to topological difference. Under a near-threshold condition, we found again the LH superiority for topological discrimination: Percentages of correct response were higher for the ring–disk pair presented in the RVF than for the pair presented in the LVF; in contrast, no lateralization was found in discriminating the topological equivalents pairs of triangle–disk and the square–disk (Fig. 1*G*) [the interactions of task and hemisphere: $F_{(1,9)} = 5.58$, $P < 0.03$ (for the ring–disk and the square–disk), and $F_{(1,9)} = 3.78$, $P = 0.06$ (for the ring–disk and the triangle–disk)].

Left-Handers Showed RH-Topology Superiority Opposite to That of Right-Handers. A basic issue in the study of hemispheric specialization concerns the relation between lateralization and handedness. Experiments 8A and 8B tested 12 and 20 left-handers for the topological lateralization, respectively. To confirm that the degree and direction of lateralization shown by the left-handers were caused by handedness rather than possible artifacts, an additional 12 and 20 right-handed subjects were also tested under exactly the same conditions of experiments 8A and 8B. The stimuli and procedures were similar to those in experiments 1 and 5, respectively, and they were designed to test two kinds of topological properties of holes and inside/outside relation. Fig. 1 *Ha* and *Hb* show the results obtained from the left-handers and right-handers, respectively. The triangle–arrow pair task generated marginally significant right lateralization, and no lateralization was found with the orientation task [the interaction of task and hemisphere: $F_{(1,11)} = 0.07$, $P > 0.7$]. Even though no significant interaction of task and hemisphere was found, the LH specialization for the triangle–arrow pair was replicated by the right-handers [the interaction of task and hemisphere: $F_{(1,11)} = 8.44$, $P < 0.02$] in the opposite direction of lateralization compared with the left-handers, indicating the interaction of handedness and hemisphere. Moreover, in experiment 8B, as shown in Fig. 1 *Hc* and *Hd*, the left-handed subjects revealed a strong LH specialization for the inside/outside relation, and no asymmetry of the distance task was found [the interaction of task (as a between-subjects factor) and hemisphere: $F_{(1,18)} = 6.70$, $P < 0.02$] opposite to the direction of lateralization found with the right-handers [the interaction of task (as a between-subjects factor) and hemisphere: $F_{(1,18)} = 12.00$, $P < 0.004$].

In summary, although left-handers did not show significant asymmetry for local features of both orientation and distance, unlike the right-handers, they did show the RH specialization for topological perception, in the opposite direction of lateralization compared with the right-handers.

Neural Correlate of LH-Topology Lateralization: An fMRI Study. For revealing the neural correlate of the LH specialization for topological properties, we investigated cortical areas mediating the topological lateralization in an fMRI study with two conditions.

Condition A. The triangle–arrow pair and control stimulus used in experiment 1 were adopted as the activation task and the baseline task, respectively. As emphasized before, these stimuli were identical in line segments and their local features. Thus, the activation task engages the topological discrimination, and the baseline task engages all but this topological discrimination. The neural correlate of the topological discrimination was thus revealed by subtracting the activity during the baseline task from that during the activation task. The fMRI results (Fig. 2*A*) showed that only a region in the left temporal gyrus (IT) was consistently more activated across subjects in the topological discrimination task (Talairach coordinates: −56, −20, −14; BA 21/20) ($n = 15$, $P < 0.0001$, random effects uncorrected; size >30 voxels), consistent with the LH specialization for topological properties found by the behavioral experiments. The LH lateralization seen in the group analysis was highly consistent across the subjects: 14 of the 15 subjects showed activation in the left IT clustered around the ROI identified in the group analysis, as shown by the green dots in Fig. 2*F* (significant peaks of activation in individual subject scans have a standard deviation of ≈15 mm). Furthermore, as shown in the average time course from those active loci (Fig. 2*D*), the triangle–arrow pair generated significantly stronger PSC (percent signal change) than the baseline stimulus.

Condition B. To test the generality of the fMRI results, we also measured the neural correlate of the topological lateralization with one more pair of stimuli. The activation task and the baseline were the same ring–**S** pair and control stimulus as those used in experiment 3, respectively. The ring–**S** pair was designed to represent the topological difference in holes with control for various nontopological features. The baseline task was, therefore, presumed to activate nearly all but the topological discrimination. As shown in Fig. 2*B*, the enhanced activation for topological discrimination in condition B also fell in a very similar region in the left IT (Talairach coordinates: −58, −18, −20; BA 20) ($n = 12$, $P < 0.0001$, random effects uncorrected; size >30 voxels) to that found in condition A. There is also a high degree of consistency across subjects (observed in 12 of 12 subjects) as shown by the red dots (the standard deviation of the activation loci is ≈10 mm) in Fig. 2*F*. The average time course from those active loci is shown in Fig. 2*E*. Similarly, the ring–**S** pair generated significantly stronger PSC in comparison with the baseline.

The convergence from condition A and B: The topological category vs. the local geometric category. From the perspective of a more abstract level of analysis, the triangle–arrow pair and the "ring–**S** pair" each represents a case of the topological difference, and the baseline stimuli based on orientation and mirror symmetry each represents a case of the local geometric difference. Thus, the triangle–arrow pair and the ring–**S** pair were both categorized as

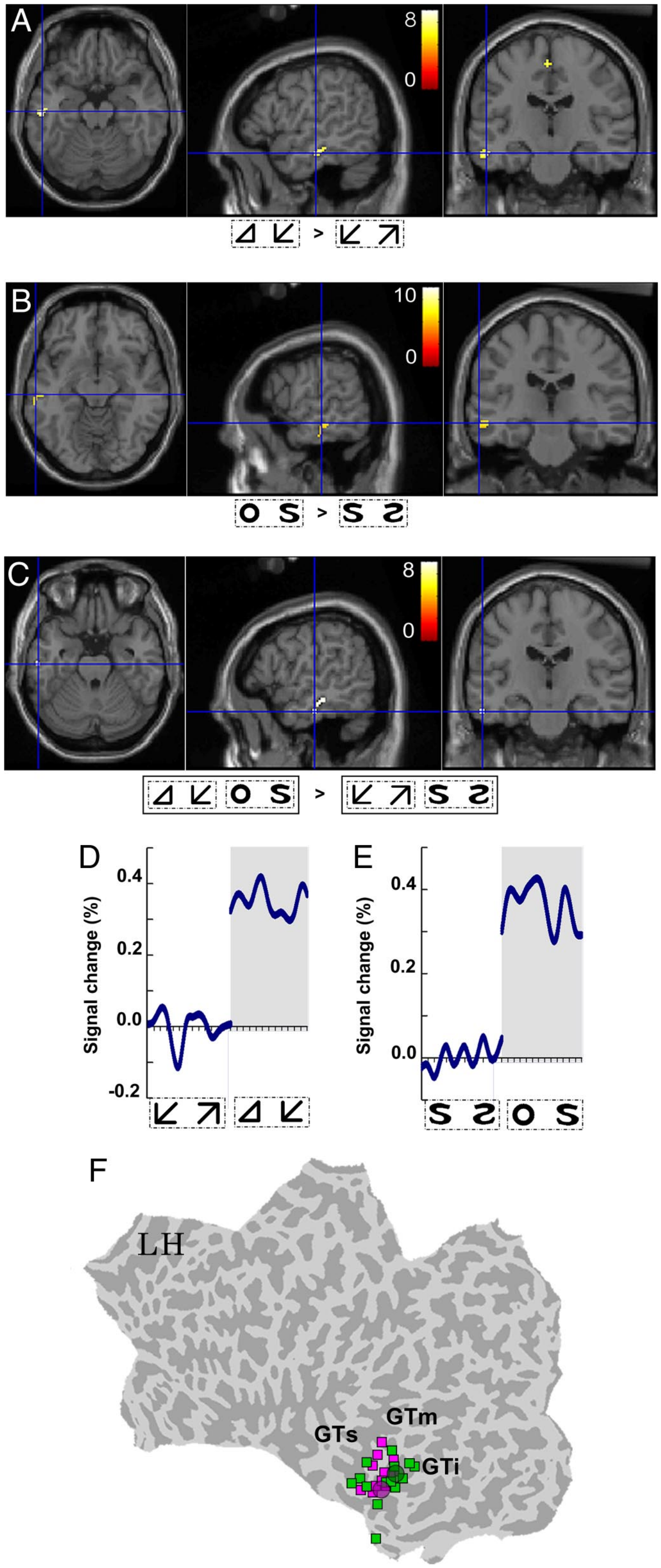

Fig. 2. Results of the fMRI study. (*A–C*) fMRI activation loci in conditions A and B and the condition of topological category vs. local geometric category, respectively. (*D* and *E*) The two time courses of fMRI signal changes in conditions A and B [$t_{(1,13)} = 9.88$, $P = 3 \times 10^{-7}$, and $t_{(1,11)} = 4.69$, $P = 6.6 \times 10^{-4}$]. (*F*) Significant peaks of activation loci identified in 15 individual subjects (green squares) and in a group analysis (larger green circle) in condition A, and in 12 individual subjects (magenta squares) and in a group analysis (larger magenta circle) in condition B; peaks are projected on the IT area of a flattened LH cortical surface of an average template brain.

the topological category, and the two baseline stimuli were used as the local geometric category in an additional data analysis.

Such convergence from condition A and B revealed that the activation loci to the topological perception are consistently located in the left IT (Talairach coordinates: −56, −24, −10 and −58, −18, −18) ($n = 27$, $P < 0.05$, random effects corrected), which is essentially the same location as that revealed in the separate analysis of conditions A and B (Fig. 2*C*).

Discussion

The main conclusion is that for right-handers, the LH is reliably and consistently superior to the RH for the global topological perception.

This conclusion was well established by converging evidence from a variety of paradigms and techniques. The topological account of lateralization was generalized to different kinds of topological properties, including the number of holes, inside/outside relation, and the global invariant of presence vs. absence. Also, the holes presented in the stimuli differ in shapes (triangular, circular, square, and diamond holes), indicating that the holes perceived as an abstract topological entity contributed to the LH specialization. Furthermore, to demonstrate the topological specificity of the LH superiority, this topological lateralization was tested systematically against a broad spectrum of local geometric properties, involved orientation, distance, size, mirror-symmetry, parallelism, and collinearity.

A major challenge to the study of the topological perception is that there can be no two figures that differ only in topological properties, without any differences in local features. Thus, one cannot test for the role of topological differences in hemispheric specialization in complete isolation. We minimized the problem through careful design of the stimuli to prevent subjects from using nontopological properties, including line segments, spatial frequency components, terminators, angles, intersections, perimeter length, and the number of edges crossed while scanning a figure, to perform the topological tasks. These nontopological features cannot, therefore, explain consistently the LH superiority. The topological account is the only one that explains, in a unified manner across all stimulus pairs used, the LH superiority.

One of major concerns in the study of hemispheric asymmetry is about the role of task factors and input factors in the lateral *t*-scope presentation of stimuli (18). The left lateralization of topological perception was supported by converging evidence obtained after taking care of a number of such task factors, including response latency vs. accuracy, stimulus detection vs. recognition (or localization), simultaneous vs. sequential judgment, and vertical vs. horizontal presentation. For instance, although experiments 1–6 used RT, experiment 7 used response accuracy. Despite the fact that response accuracy is sometimes considered less sensitive than RT as an index for lateralization (18), our results obtained with the measure of accuracy still demonstrated a robust pattern of the left topological lateralization.

It is generally held that left-handers, even in the most well established lateralization of speech production, are more variable than right-handers in both the degree and the direction of hemispheric specialization (19). Most studies of hemispheric specialization, therefore, controlled for possible atypical lateralization in left-handers by focusing their investigations on right-handers. Nevertheless, experiment 8 found that, unlike the right-handers, although the left-handers did not show significant lateralization of local features, they still showed a clear-cut lateralization of topological perception, but it was in an opposite direction compared with the right-handers. This fact indicates the fundamental role of topological properties in determining the hemispheric asymmetry.

In the following, we will discuss the relation of the global-first topological theory to other existing theories on hemispheric asymmetry, including the global precedence hypothesis (2–9), the dichotomy of "categorical vs. coordinate" spatial relations (20), the dichotomy of "higher vs. lower spatial frequencies" (21), and the task difficulty hypothesis (22).

The global precedence paradigm provides an operational technique to examine the relation between whole and part. However, there is no reason to claim, for example, that a face would be perceived earlier than either its eye or mouth. Nevertheless, we are able to claim that holistic registration, which determines which two eyes and which mouth belong to the same face, takes place before the recognition of this face. That is, the perception of global topological invariant of connectivity of the face (a connected entity as a face) is before the perception of detailed properties of the face. The performance advantage for compound forms may be due to the fact that grouping based on proximity is before grouping based on similarity of local features (11). A previous study reported a dominant role for proximity, after carefully dissociating proximity from physical similarity (23). Furthermore, from the topological definition of "global" and "local," a compound (or whole) form (e.g., a compound arrow composed of component triangles) may possess its own global properties of connectivity as well as its own local properties of orientation, whereas the component triangle may possess its own local properties of orientation as well as its own global properties of having a hole. Given this topological definition of "global" and "local" in place of "whole" (or "compound") and "part" (or "component"), we can now describe global precedence in a precise way: That is, "global topological perception is *prior* to perception of other local geometric properties" (11). Indeed, our results support the idea that the topological definition of "global" and "local" has psychological validity in characterizing the hemispheric specialization.

Another popular hypothesis is related to the hemispheric dichotomy of categorical vs. coordinate relations: The LH is specialized for categorical processing, whereas the RH is specialized for coordinate processing (20). It is obvious that the global topological properties are types of categorical concepts. However, it is equally obvious that most local geometric properties, such as mirror-symmetry, parallelism, and collinearity, must also be considered categorical rather than coordinate relations. Nevertheless, these geometric properties were shown here to have a RH advantage, opposite to the prediction by the categorical vs. coordinate dichotomy. The main evidence for the dichotomy of categorical vs. coordinate came from an experiment in which subjects demonstrated the LH advantage for the "on/off" relation, and in contrast, the RH advantage for the "near/far" relation (20). When a dot is located "off" a hollow figure, it corresponds to "outside" in the topological relation of inside/outside. However, when the dot is located "on" a hollow figure, the task becomes the discrimination of shapes formed by conjoining the dot with the hollow figure. The on/off relation, therefore, partly involves a topological property and partly, a local geometric property. It becomes understandable that whereas we revealed the clear-cut LH advantage for the inside/outside detection, there was only a marginal advantage for the on/off detection (20), as the on/off relation reflects only partly the topological perception. In sum, although the dichotomy of categorical/coordinate does not sufficiently capture the topological structure in hemispheric specialization, the topological approach may provide a pertinent and comprehensive account for the data from the study of on/off vs. near/far relations.

The spatial frequency hypothesis for lateralization documented one more popular dichotomy, namely the asymmetry of LH-high/RH-low spatial frequency. However, our experiments, which explicitly manipulated the spatial frequencies of stimuli, render the variables based on spatial frequency components not to be relevant to the LH lateralization for topological perception. It is obvious that there is no sizable difference of the triangle–arrow in spatial frequency components; and the difference in 2D

Fourier power spectra between the ring–**S** are much too small to determine the LH superiority (15).

Finally, let us discuss a concern about the factor of task difficulty. It was argued that because RH simply may be better in performing more difficult tasks, the LH specialization for categorical processing may be just due to the fact that categorical judgments would be easier than coordinate judgments (20, 22). However, this argument is simply not applicable to the topological vs. local geometric tasks, as topological and local geometric properties should all be considered as categorical relations. Previous empirical studies already systematically manipulated task difficulty for both categorical and coordinate tasks, and they found no evidence for an effect of task difficulty *per se* (20). In addition, as found in the global precedence hypothesis, the task to perceive compound letters took shorter RT than those to perceive component letters, but it generated the RH dominance—exactly contradicting the task difficulty account. Thus, the factor of task difficulty cannot be a main concern for control in the present study. Nevertheless, it is worth pointing out that experiment 5 demonstrated that, although there is no significant difference in the RTs between the two tasks, there is still clear-cut LH superiority for inside/outside relation. In short, the concept of task difficulty factor is ill-defined and does not present a valid interpretation for the LH superiority for the topological properties.

The fMRI activation in the left IT further substantiates the behavioral finding of the LH superiority for topological perception. Particularly, the two activation stimuli of the triangle–arrow and the ring–**S** were chosen to measure cortical activation common to the two tasks, which share the topological property in holes but differ greatly in local features. The neural correlate of the common cognitive component of topological discrimination in the two fMRI conditions, namely the overlapping and conjunctional activation loci in the left IT revealed across individual subjects and conditions, strengthens the conclusion that it is indeed the topological perception that evidences the LH superiority.

Methods

The handedness of the subjects was measured with the handedness questionnaire for the Chinese population (24). All subjects had a left-to-right reading habit.

Samples of photographic reductions of the original stimuli are shown in Fig. 1 *A*–*G*, which were laterally presented, with their most central edges (or imaginary edges) located away from the central fixation point by 3.5° (in experiments 1, 2, 4, 6, and 8a), 4° (in experiment 3), 3.2° (in experiments 5 and 8b), or 1.9° (in experiment 7).

In experiments 1–6 and 8, each trial began with a central fixation point for ≈1 s, followed by a stimulus for 150 ms. In experiments 1 and 8a, subjects detected whether a quadrant is different from the other three. In experiments 2–4 and 6, subjects judged which quadrant was different from the other three. In experiments 5 and 8b, subjects in one group detected inside/outside, and another group detected near/far. The sequences of trials were randomized, and the orders of the LVF and RVF presentations, the right-hand and left-hand response, and the task-to-button correspondence were all counterbalanced across the subjects. Subjects performed accurately in general without showing any speed–accuracy trade-off and any significant hemispheric asymmetry in error rates in experiments 1–6 and 8. Only RTs for correct trials thus were subject to ANOVA.

fMRI Study. Sixteen right-handers with a left-to-right reading habit participated in the study. Fifteen of them were scanned in condition A, and 12 of them were scanned in condition B (with 11 of them in both conditions A and B). The stimuli in conditions A and B were similar to those used in experiments 1 and 3, respectively, and presented centrally at the viewing distance of 60 cm.

See supporting information (SI) *Methods* and SI Fig. 3 for more details about the methods used.

ACKNOWLEDGMENTS. This research was supported by Ministry of Science and Technology of China Grants 2005CB522800 and 2004CB318101, National Nature Science Foundation of China Grant 30621004, and Knowledge Innovation Projects of Chinese Academy of Sciences (L.C.). Z. Lan participated in parts of the experiments.

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