

Contributions of the Visual Ventral Pathway to Long-Range Apparent Motion

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Objects displaced intermittently across the visual field will nonetheless give an illusion of continuous motion [called apparent motion (AM)] under many common conditions. It is believed that form perception is of minor importance in determining AM, and that AM is mediated by motion-sensitive areas in the “where” pathway of the cortex. However, form and motion typically interact in specific ways when natural objects move through the environment. We used functional magnetic resonance imaging to measure cortical activation to long-range AM, compared to short-range AM and flicker, while we varied stability of structural differences between forms. Long-range AM activated the anterior-temporal lobe in the visual ventral pathway, and the response varied according to the form stability. The results suggest that long-range AM is associated with neural systems for form perception.

AM, like real motion, is a common phenomenon in everyday life, including the motion created in films, television, and neon advertisements. The illusion of motion is created by discrete alternation in position of “motionless” forms. A long-standing and fundamental question in motion perception is whether AM is equivalent to real motion (1). The current dominant view considers AM to be detected by the same visual channels as real motion (1), with form vision playing at best a minor role. In particular, it is thought that structural forms are not the correspondence tokens in AM (2). Recent neuroimaging studies have shown that area MT, an area important for motion perception but not form vision, is activated by both real motion (3–6) and various illusions of motion (7, 8).

However, when one views long-range AM (9) between two forms, and these forms have dissimilar shapes, one perceives not only translation and rotation but also plastic deformations of the shapes. For example, one may perceive a triangle moving and simultaneously changing its shape to become a circle or vice versa (10). Long-range AM with a plastic shape change is also commonly observed in everyday life (11).

The existence of AM under these conditions implies a motion correspondence match, in which the visual system somehow identifies an object in one display with its match in a later display, even though the object may not be identical in the two displays. The phenomenon of shape-changing transformations raises a key

question in understanding of AM, namely which invariants of an object are preserved under shape-changing transformations and are consequently used to achieve a correspondence match by the visual system (12). No one has yet devised a general-purpose theory of long-range AM that can account for its ecological functions (13). Nevertheless, this analysis of the correspondence problem in shape-changing, long-range AM led us to hypothesize that long-range AM is actually associated with global form perception (12–15).

To test this idea, we used functional magnetic resonance imaging (fMRI) to investigate human cortical areas mediating long-range AM (16). In experiment 1a (Exp. 1a), the activation stimulus was two squares separated by about 10° and presented in alternation so as to produce AM (Fig. 1A). The baseline stimulus was the same two squares but presented simultaneously, so that flicker but no AM was perceived. The data revealed activation not only in lateral occipitotemporal cortex (17) but also in the anterior temporal gyri [Talairach coordinates are (–48, –3, –32) and (50, –5, –22)] (Fig. 1, B through D). This latter result was a surprise because the anterior temporal lobe is a late destination of the visual form pathway (18), which is anatomically far removed from area MT and the “where” pathway.

Two control experiments further tested whether this activation was specific to long-range AM, as opposed to short-range AM or flicker. Exp. 1b compared activation to an individual square that was moving (in short-range AM) versus stationary, and Exp. 1c compared activation by two flickering squares versus the same single moving square. No significant activation was found in the anterior temporal gyri in these two conditions (Fig. 1, B and D), while area MT+ activated in Exp. 1b coin-

cided with the activated area in the lateral occipitotemporal cortex found in Exp. 1a and was also activated with the flickering stimuli in Exp. 1c (Fig. 1B) (6).

If this activation of the anterior temporal lobe indeed occurred because long-range AM is associated with form perception, then varying the form properties should influence the activation pattern. This prediction is related to the fundamental question of what are the primitives of visual form perception (19, 20). One important factor in evaluating potential primitives for perceptual representation of forms is their relative stability under changes (19–21). When an object in the natural environment is subjected to changes due to its motion (which may be non-rigid), or to changes of illumination, it is generally the case that some of its form properties are altered, while others remain invariant. Specifically, among these form properties, the topological properties, such as “connectivity” and the number of “holes,” are structurally most stable under changes: smooth deformations cannot create or destroy connectedness and holes, but they do alter other form properties, such as size and orientation. Exp. 2 was conducted to measure the correlation of cortical activation in AM with a range of levels of stability of structural differences between forms.

AM was produced by five pairs of figures (Fig. 2A) (22). The differences between the two figures in pairs B to E represent different levels of form stability. (The greater the stability of structural difference between the forms, the more radical the transformation required to transform one form into another.) In ascending order from pairs B to E, they differ in Euclidean geometry, affine geometry, projective geometry, and finally topology with the highest stability. These constitute a hierarchy of geometries according to Klein’s Erlangen Program, which provides a formal way to stratify geometric properties with respect to their structural stability (23). Behavioral studies found that the relative saliency of different geometric properties is remarkably consistent with this hierarchy of geometries (19–21).

The activation produced by AM, using these pairs of figures, in the anterior temporal lobe was correlated with their form stability under change (24). The activated cortical volumes as well as the amplitudes of signal changes in the anterior temporal lobe increased monotonically with increasing levels of the stability of structural differences in the forms (Fig. 2, B through D). This result suggests that as the stability of structural difference between two forms is increased, the greater the magnitude of cortical activation required to produce the perception of AM between the two forms. Specifically, pairwise comparisons by means of GLM (general linear model) analysis indicated that pair E, representing the highest stability (topological difference), caused the strongest activation in comparison with pairs D, C, and B (for activat-

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ed volumes, $P < 0.016, 0.006, 0.004$, respectively; for signal intensities, $P < 0.012, 0.001, 0.001$, respectively). Pair D, representing higher stability than pairs C and B, caused greater activation than did pairs C and B (for activated volumes, $P < 0.038, 0.019$, respectively; for signal intensities, $P < 0.006, 0.001$, respectively). Pair C, representing relatively higher stability than pair B, caused relatively greater activation than did pair B (for activated volumes, $P < 0.020$; for signal intensities, $P < 0.030$) (Fig. 2, C and D) (22).

To test whether this activation in the anterior temporal lobe is a function of the stability differences in the stimulus pairs per se but in the absence of long-range AM, the stimulus pair was presented simultaneously, so that no AM was observed between the stimuli (Exp. 3). This control experiment did not detect significant activation in anterior temporal lobe at all; therefore, the magnitude of activation is not a function of stability levels per se (for the main effect, $P > 0.2$).

Three additional experiments further tested the neural correlate of form stability and whether the activation in the anterior temporal lobe was specific to long-range AM. In Exp. 4, in producing long-range AM, two pairs of figures (25) were compared with the baseline task of two identical S-like figures (Fig. 3A). The S-like figure is topologically different from the ring in holes. However, the S-like figure was made to approximate the area of the ring. Even though the local-feature differences between the S-like figure and the ring (such as luminous flux difference, spatial frequency components, and perimeter length) were minimized (25), this topologically different pair caused stronger activation in the anterior temporal lobe than did the topologically equivalent pair of S-like figure and disk (for activated volumes, $P < 0.03$; for signal intensities, $P < 0.01$) (Fig. 3B). Their Talairach coordinates were $(-51, -7, -33)$ and $(44, 4, -31)$, and $(-43, 5, -25)$ and $(37, 16, -27)$, respectively.

Kinetic shapes (26), instead of luminance-

based ones, were used in Exp. 5 and 6. Kinetic shapes are defined solely by spatiotemporal correlations rather than luminance differences (Fig. 3C). Thus, all luminance-based features were well controlled. Recent fMRI studies found that dynamic random dots with 0% coherence produced weak activation in human MT+ (27), which makes the kinetic shapes a particularly good choice to control for any confounding effects of differences in total motion energy. Furthermore, the similarity of the AM percepts generated by kinetic forms and luminance-contrast forms affords a test for the generality of this neural correlate of structural stability.

In Exp. 5, a kinetic disk paired with a kinetic triangle, and a kinetic disk paired with a kinetic ring (Fig. 3C), were compared with two identical kinetic disks, all producing long-range AM. The anterior temporal lobe was activated more strongly by the kinetic forms differing in holes (for activated volumes, $P < 0.04$; for signal intensities, $P < 0.01$) (Fig. 3D), similar to what we found with luminance-defined patterns, even

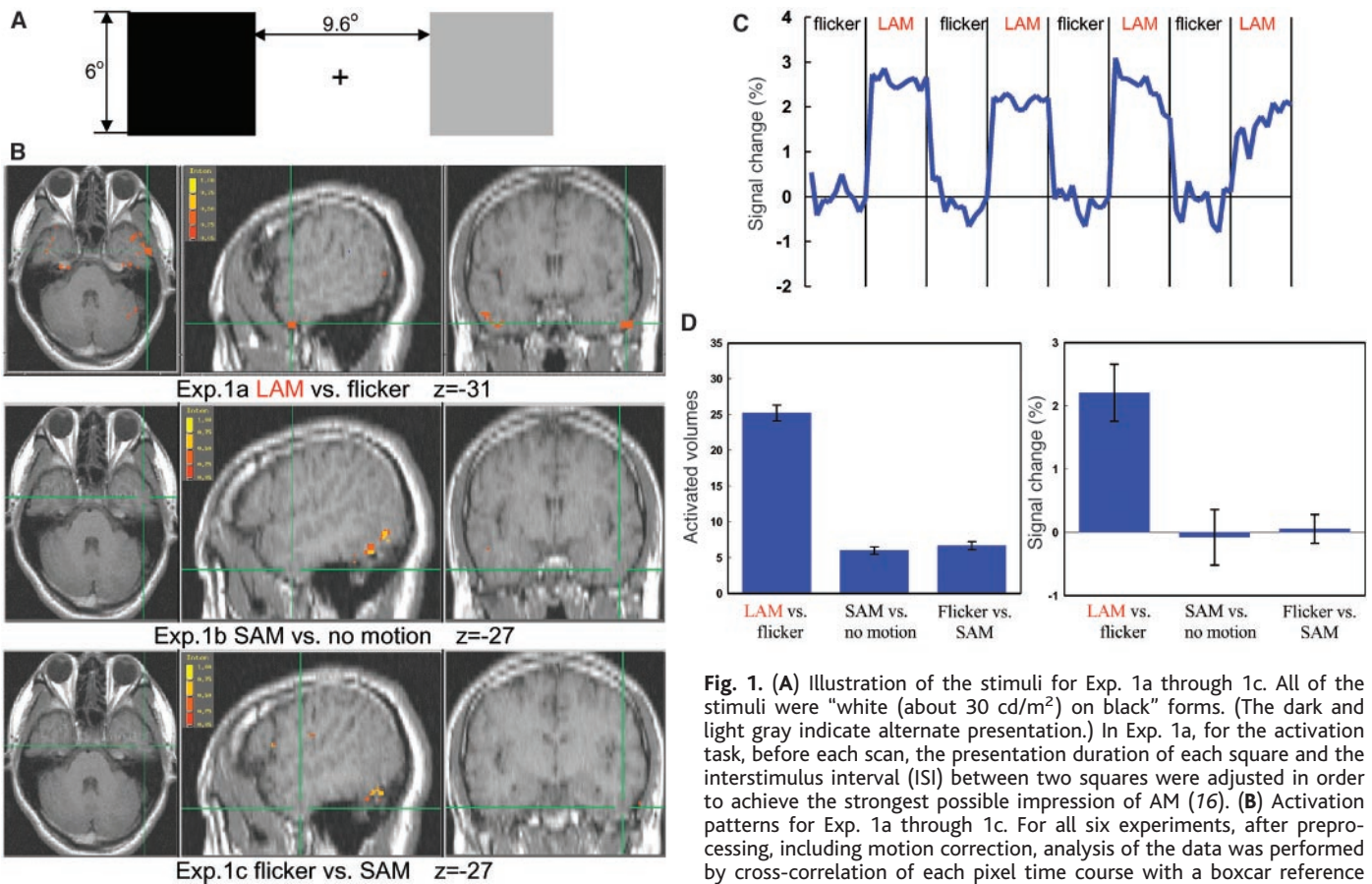


Fig. 1. (A) Illustration of the stimuli for Exp. 1a through 1c. All of the stimuli were "white (about 30 cd/m²) on black" forms. (The dark and light gray indicate alternate presentation.) In Exp. 1a, for the activation task, before each scan, the presentation duration of each square and the interstimulus interval (ISI) between two squares were adjusted in order to achieve the strongest possible impression of AM (16). (B) Activation patterns for Exp. 1a through 1c. For all six experiments, after preprocessing, including motion correction, analysis of the data was performed by cross-correlation of each pixel time course with a boxcar reference function to obtain correlation coefficient maps for each single participant (11, 11, 7, 7, 6, and 11 in Exp. 1 through 6, respectively) ($r > 0.30, P < 0.01$) to generate averaged correlation coefficient maps by analysis of functional neuroimaging images (AFNI) (30). Activation was also found in and near the calcarine sulcus in each experiment. The patterns of activation are quite evident for individual participants, except for one in Exp. 1a. LAM, long-range AM; SAM, short-range AM. (C) The time courses of signal change, averaged over the 11 participants responding to AM in the anterior temporal lobe. (D) The histograms of activation volumes and amplitudes of signal change, averaged over the 11 participants in the anterior temporal lobe. The activation areas are characterized by mean activated cortical volumes (the number of voxels each with the size of 3.9 mm by 3.9 mm by 7 mm). The anterior temporal lobe is delimited as the anterior segment of the temporal gyri extending from the temporal pole to the coronal sector through the posterior commissure. No significant lateralization was observed. aGT, anterior temporal lobe.

though the hole was defined solely by spatio-temporal correlation. Their Talairach coordinates are (-44, 1, -26) and (46, 5, -33), and (-40, 7, -27) and (43, 6, -24), respectively.

With respect to kinetic forms, another characteristic is worth emphasizing. Although kinetic shapes defined by static random dots against a background of dynamic noise can produce AM, shapes defined by dynamic dots against a background of static random dots (pair A versus pair B in Fig. 3E) produce no AM at all (26). In the experiments using luminance-contrast forms, two figures must be presented alternately in order to produce AM. To use the same two figures as a baseline condition that controls for possible confounds (for example, luminance flux) but without involving any AM, one normally has to present the two fig-

ures simultaneously. Therefore, by limiting the stimuli to luminance-contrast forms, it would be difficult to equate both spatial and temporal aspects of stimulus presentation between the two conditions.

In Exp. 6, we made use of this asymmetry in AM to provide some additional controls for presentation conditions. The activation task of two kinetic squares was compared with the baseline task of the same two kinetic squares except with the relation of figure and surround reversed (Fig. 3E). Because the kinetic forms in the baseline condition produced no AM at all, the task and baseline stimuli could be presented with almost identical presentation conditions. Comparing the two conditions, significant activation by AM was still found in the anterior temporal gyri [Talairach coordinates (-39, -5, -27) and (51,

-8, -25)]; no significant difference in activation in area MT+ was found between the AM and no AM conditions (Fig. 3, F and G). This result is not unique to one displacement distance (9.6°). When we repeated the same activation and base tasks with distances of 7°, 5°, and 3°, we consistently found significant activation in the anterior temporal gyri.

Finally, although participants were instructed to maintain fixation during the tasks, we considered the possibility that the activation patterns found in the anterior temporal gyri were due to eye movements (28). As an additional control, we measured eye movements outside of the magnet in four of the participants in the fMRI studies. Under all of the conditions with the stimuli representing different levels of structural stability, all of the participants showed reliable fixation, and no appreciable eye movements were detected.

In conclusion, the finding that long-range AM primarily activated the anterior temporal lobe suggests a dissociation between long-range AM and short-range AM. This is consistent with distinct motion systems hypothesized by the "dual process theory" (29) and the theory of "three motion systems" (15). It is further strengthened because the activated cortical volumes and amplitudes of signal change increased monotonically with increasing levels of the stability of structural differences between the forms during AM. This systematic neural correlate of form stability suggests that long-range AM is associated with neural system for form perception, and argues against the common belief that figural properties are of little importance in determining AM (2, 14). The involvement of the form pathway in long-range AM raises interesting issues about the relation between the two visual pathways. Regarding the function of long-range AM, these neuroimaging findings support an idea suggested by behavioral findings of topological preference in AM reported about 20 years ago (12), that long-range AM may work by abstracting invariants of form.

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9. "Short-range" refers to small displacement (less than, typically, 0.25° of visual angle) and rapid alternation (less than 80 ms/frame), whereas "long-range" refers to larger displacement and slower alternation (30). Short-range AM appears to coincide with image-level processing of motion; long-range AM is more naturally associated with form-level processing (13).
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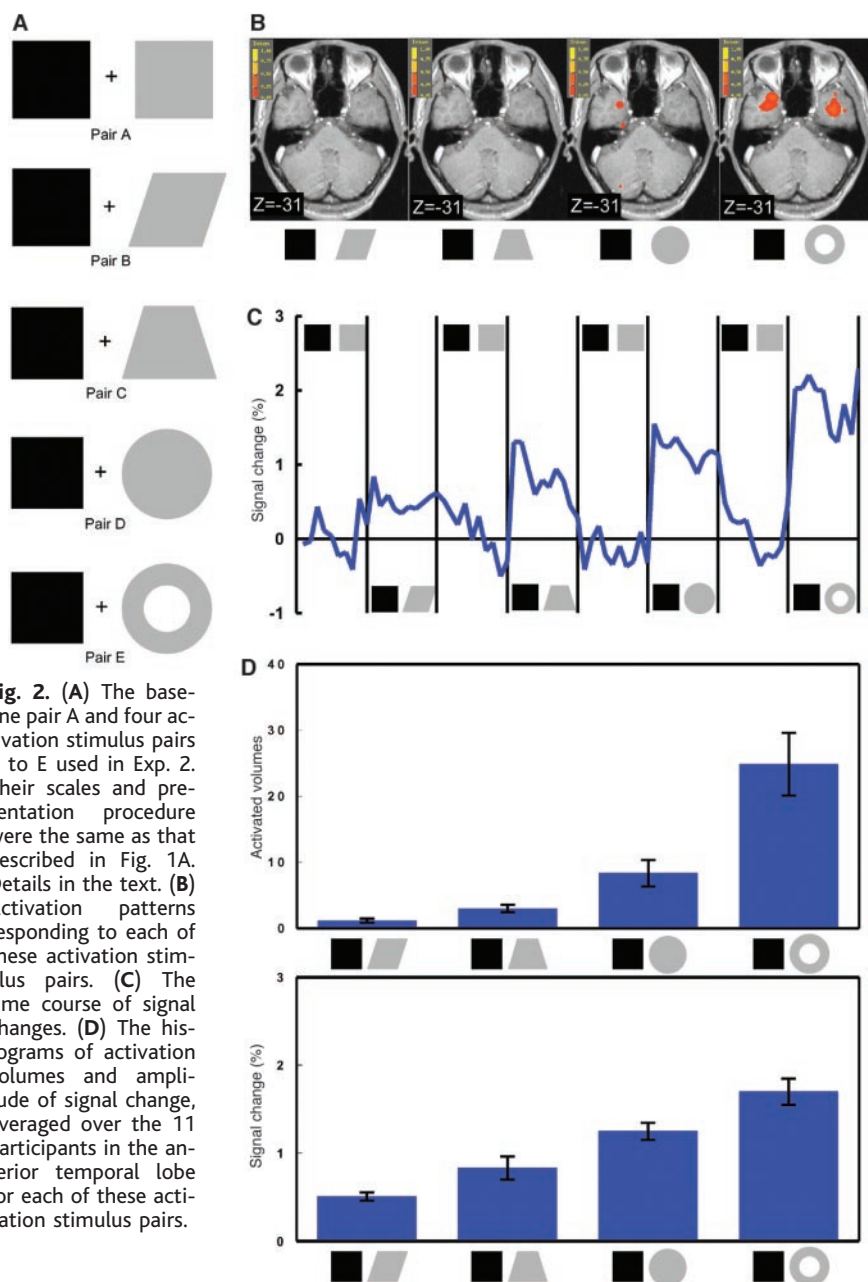


Fig. 2. (A) The baseline pair A and four activation stimulus pairs B to E used in Exp. 2. Their scales and presentation procedure were the same as that described in Fig. 1A. Details in the text. (B) Activation patterns responding to each of these activation stimulus pairs. (C) The time course of signal changes. (D) The histograms of activation volumes and amplitude of signal change, averaged over the 11 participants in the anterior temporal lobe for each of these activation stimulus pairs.

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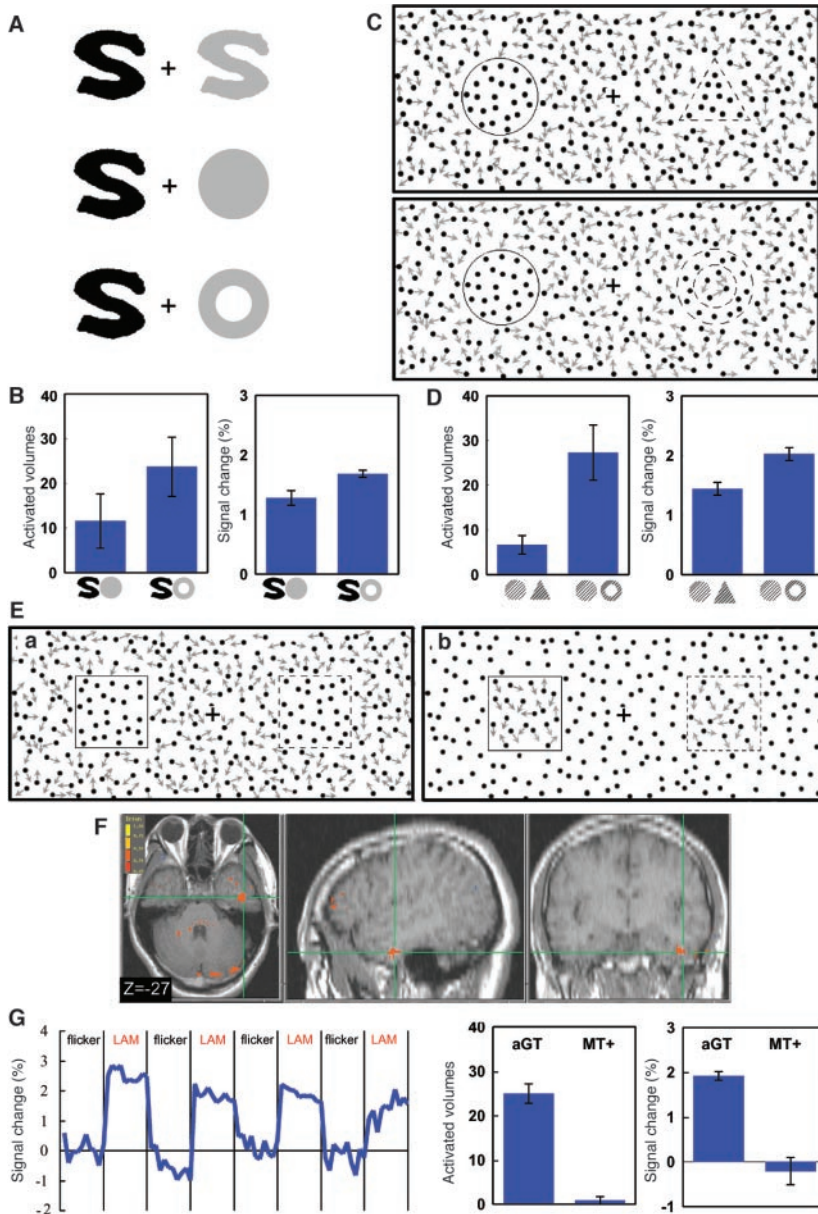


Fig. 3. (A) Illustration of the baseline stimulus and two activation stimuli used in Exp. 4, with the same scales and presentation procedure as that described in Fig. 1A. (B) The histograms of activation volumes and amplitudes of signal change for each of the activation stimulus pairs, in the anterior temporal lobe. (C) Illustration of kinetic forms used as the activation stimuli in Exp. 5. Their scales and presentation procedure are the same as that described in Fig. 1A, except that their duration and ISI used were about 240 to 320 ms and 30 to 70 ms, respectively. The random dots in each of the successive frames were white with equal probability. The continuous and dotted lines indicated the subjective contour of the kinetic forms in the initial and alternate presentations. (D) The histograms of amplitudes of signal change and activation volumes, in the anterior temporal lobe. (E) Illustration of kinetic forms used in Exp. 6. Pair A (a) was used as the activation stimulus, and pair B (b), the baseline. In pair A, the figure is dynamic and the surround static; in pair B, the figure is static and the surround is dynamic. The observation that pair B would not produce AM was confirmed for each of the 11 participants scanned. (F) The activation pattern responding to pair A. (G) The time course of signal change averaged over the 11 participants responding to long-range AM in the anterior temporal lobe, and the histograms of activation volumes and amplitudes of signal change, in the anterior temporal lobe and area MT+.

11. For example, when an animal runs behind a sizable occluder (such as a large trunk) and has a somewhat different shape when emerging on the opposite side, our normal perception is that, despite its changes of shape, it undergoes smooth motion and preserves its identity over time.
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 22. The five pairs of figures used in Exp. 2 are as follows: A, two identical squares (the baseline); B, a square versus a parallelogram; C, a square versus a trapezoid; D, a square versus a solid circle; and E, a square versus a ring. The Talairach coordinates of activation with pairs B, C, D, and E are (–42, –9, –23) and (40, –3, –18), (–41, –6, –27) and (41, –6, –24), (–38, –5, –26) and (42, –7, –24), and (–36, –9, –24) and (39, –10, –24), respectively.
 23. The mathematician Klein, in 1872, proposed a general principle for constructing different geometries that is now known as the Erlangen Program, in which arbitrary mathematical groups of transformations were applied to describe the geometrical invariants of forms under changes. Using this principle, Klein built a hierarchy of geometries, stratified in ascending order of stability: Euclidean geometry, affine geometry, projective geometry, and finally topology with the highest stability. Levels of relative structural stability of various figural properties can be described and stratified systematically and in a formal, precise way in terms of invariants at different geometric levels defined by this program.
 24. Neuroimaging studies have found bilateral anterior temporal cortical activations in association with object recognition (31), natural objects naming and matching (32, 33), face identification (34, 35), visual discrimination tasks with faces and words (36), and classification of objects across levels (37). From these studies, it is clear that cortical areas for object recognition extend far into the anterior temporal cortex, even though the precise relation between cortical regions identified in these earlier studies of form vision and the temporal cortical region we have identified in the present study is not yet known.
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 28. Recent fMRI studies found that eye movements as well as attentive tracking and discrete attention shifts produce activations mainly in parietal and frontal regions as well as precuneus and area MT+, which are anatomically distant from the anterior temporal lobe (aGT) (40, 41).
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 Materials and Methods

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