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Perceptual Continuity and the Emergence of Perceptual Persistence in the Ventral Visual Pathway

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Large, Mary-Ellen, Adrian Aldcroft, and Tutis Vilis. Perceptual continuity and the emergence of perceptual persistence in the ventral visual pathway. *J Neurophysiol* 93: 3453–3462, 2005. First published January 19, 2005; doi:10.1152/jn.00934.2004. Perceptual continuity is an important aspect of our experience of the visual world. In this study, we focus on an example of perceptual continuity involving the maintenance of figure–ground segregation despite the removal of binding cues that initiated the segregation. Fragmented line drawings of objects were superimposed on a background of randomly oriented lines. Global forms could be discriminated from the background based on differences in motion or differences in color/brightness. Furthermore, perception of a global form persisted after the binding cue had been removed. A comparison between the persistence of forms constructed from motion or color demonstrated that both forms produced persistence after the object defining cues were removed. Functional imaging showed a gradual increase in the persistence of brain activity in the lower visual areas (V1, V2, VP), which reached significance in V4v and peaked in the lateral occipital area. There was no difference in the location of persistence for color- or motion-defined forms. These results suggest that the retention of a global percept is an emerging property of the ventral visual processing stream and the maintenance of grouped visual elements is independent of cue type. We postulated that perceptual persistence depends on a system of perceptual memory reflecting the state of perceptual organization.

INTRODUCTION

William James (Hock et al. 2003) characterized our sensory experience as one of "blooming, buzzing confusion." Our everyday experience of the natural environment, however, is one in which our percepts remain stable despite disruptions caused by transient changes in the environment such as movement or changes in illumination. Conversely, transient changes in low-level properties, like color and motion, can enhance the detection of objects in the environment. The percept of those objects can remain stable for some time after the revealing cues are no longer present. For example, a camouflaged animal might not be noticed until it moves, but once it has moved, it becomes clearly visible, and can remain so when it resumes a fixed position. A number of psychophysical experiments have investigated phenomena related to perceptual continuity such as perceptual hysteresis for bistable stimuli (Hock et al. 1993; Leopold et al. 2002; Maier et al. 2003; Sekuler 1996; Suzuki and Peterson 2000; Williams et al. 1986; Yantis and Nakama 1998). However, the neural processes that underlie perceptual continuity are not well understood. In this study, we focused on a particular form of perceptual persistence first reported by

Regan (1986, 2000). He demonstrated that fragmented line drawings of objects could be discriminated from a background of randomly oriented lines based on differences in motion. When the motion cue was removed, the percept of the object persisted before fading into the background. Using functional imaging, our aim was to explore the role of the ventral visual stream in the maintenance of global percepts after the removal of binding cues that initiated figure–ground segregation. In addition, we examined whether the persistence of a global percept was independent of the cue used to bind local features into global configurations.

There are two critical stages to the perceptual persistence described by Regan (1986, 2000): an initial stage, which segregates visual elements into figure and ground; and a second stage, which maintains the segregation in the absence of a binding cue. For a percept to be sustained despite the removal of binding cues there must be a period of time in which the representation of the percept is dissociated from sensory input. Ferber et al. (2005) proposed that area LO (lateral occipital area, part of the lateral occipital complex that lies immediately posterior to middle temporal area, MT+) is a locus for the retention of the initial percept and plays an intermediate role between sensory memory and short-term memory. In their study, Ferber et al. (2005; see also Ferber et al. 2003) investigated whether the behavioral persistence of an object percept would be reflected as persistence in brain activation in the lateral occipital complex (LOC), defined as an object-sensitive area (Grill-Spector et al. 1999, 2001, 2003; James et al. 2000; Kanwisher et al. 1996; Malach et al. 1995; among many others) or in MT+, defined as a motion-sensitive area (Tootell et al. 1995; Watson et al. 1993; Zeki et al. 1991), or perhaps in both areas. They found that brain activation persisted in area LO but not in area MT+. Ferber et al. (2005) concluded that LO is activated by grouping processes and is responsible for maintaining the integration of the visual elements. Importantly, Ferber et al. (2005) tested whether persistence in brain activation would occur when new object fragments were substituted for those fragments that were initially grouped together based on motion. They found that LO can maintain a percept even in the absence of fragments that had been previously bound together to form the object, suggesting that the representation of the object in LO must be somewhat abstracted from the input representation generated by sensory signals.

In support of Ferber et al.'s contention that area LO subserves the persistence of a percept, Kleinschmidt et al. (2002)

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also found that LOC was involved in the maintenance of an object percept. In Kleinschmidt et al.'s study a letter was segregated from the background by gradually increasing its contrast relative to the background (pop out). The contrast was then decreased until the letter was no longer visible (drop out). The threshold at which pop out occurred was higher than the threshold for drop out (perceptual hysteresis). Subsequent analysis of the functionalized magnetic resonance imaging (fMRI) signal revealed a relative increase in neural activity in LOC for trials with perceptual hysteresis. Kleinschmidt et al. also found patterns of activity in the medial temporal cortex that were sustained during perceptual hysteresis. They suggested that the patterns of activity in these 2 cortical areas reflects top-down processes involving memory signals used to stabilize the percept in the face of degradation.

Whereas Ferber et al. (2005) and Kleinschmidt et al. (2002) suggest that perceptual persistence is mediated by areas beyond the early visual cortex, some psychophysical studies suggest otherwise. For example, Magnusson and Greenlee (1999; Magnusson 2000) proposed a form of perceptual memory that codes for basic visual attributes (color, motion, orientation, contrast, etc.) using a series of parallel memory stores. These memory processes are located early in the visual processing hierarchy and provide inputs to higher-order systems that code for the structure of objects. Using functional imaging, our study investigates whether lower visual areas are involved in the maintenance of global percepts after the removal of binding cue. In addition, because the model of perceptual memory is characterized as having parallel memory stores specialized for single stimulus dimensions, we examined whether the persistence of brain activation to fragmented line drawings of objects constructed from motion differed from the persistence associated with line drawings constructed from color/brightness similarities between the fragments composing the objects and those composing the background.

METHODS

Subjects

Seven healthy volunteers (5 male, 2 female) participated in this study. All subjects gave written consent and all procedures were approved by the University of Western Ontario Ethics Review Board.

fMRI

Experiments were performed in a 4.0-Tesla Varian Siemens whole-body imaging system. Data from 4 subjects were collected using a navigator echo–corrected T2*-weighted segmented gradient echo planar pulse sequence (EPI). Data from the other subjects were collected using an interleaved, 2-segment, optimized spiral imaging sequence with the same parameters. A 15.5×11.5-cm quadrature radio frequency surface coil placed at the occipital pole was used to improve the signal-to-noise ratio. Functional data were aligned to high-resolution inversion–prepared 3-D T1*-weighted anatomical images of the brain collected immediately after the functional images using the same in-plane field of view (FOV). The parameters for the EPI sequence anatomicals were 64 slices, echo time (TE) = 5.3 ms, repetition time (TR) = 9.8 ms, inversion time (TI) = 600 ms, in-plane pixel size = 0.75×0.75 mm, slice thickness = 2.5 mm. The parameters for the spiral sequence anatomicals were 96 slices, TE = 3 ms, TR = 50 ms, TI = 1,300 ms, in-plane pixel size = 0.75×0.75 mm, slice thickness = 1.25 mm.

Experimental protocol

Subjects viewed, through a mirror, images that were back-projected onto a screen. The display extended 45° horizontally and 20° vertically. In all experiments the subjects fixated centrally on a stationary dot. The parameters for the MT+ and LO scans were FOV = 19.2×19.2 cm; in-plane pixel size 3×3 mm; TE = 15 ms; volume acquisition time, 2 s; FA = 40°; 11 slices; slice thickness, 5 mm. The slices were oriented approximately parallel to the calcarine sulcus and included MT+ and the adjacent LO. Measures of persistence require a high temporal resolution. To allow for a volume acquisition time of 0.5 s, only 5 contiguous slices (FOV = 19.2×19.2 cm; in-plane pixel size 3×3 mm; TE = 15 ms; FA = 40°; slice thickness = 5 mm) were selected based on the MT+ and LOC localizer scans.

MT+ localizer

To identify brain areas that are sensitive to motion, the display alternated between moving or stationary vertical black bars (height = 20°, total display width of 18 bars = 40° individual bar width 0.2°, velocity = 4°/s). The moving bars alternately moved from center screen to the edges (temporal movement) or from the edges to center screen (nasal movement). Four functional scans were performed with 18 epochs per scan. Each epoch was 16 s long.

LO localizer

To identify object-sensitive brain areas, we presented our subjects with intact 2-dimensional (2D) black and white line drawings of objects (animals, tools, and letters) alternating with scrambled versions of the same images. Three functional scans were performed with 25 epochs per scan and each epoch was 12 s long. Twelve images were presented in each epoch at 1-s intervals. To control for attention, subjects performed a one-back matching task where they pressed a response key whenever they saw 2 identical images, either intact or scrambled, in a row.

Retinotopic mapping

The location of areas V1, V2, V3, and V4 were established for each subject in a separate scanning session. To delineate the borders of the retinotopic areas, the vertical and horizontal visual field meridians were mapped. A pie-shaped wedge showing an animated movie was presented randomly to the right, left, above, or below fixation at 12-s intervals. These epochs were interspersed with 12-s epochs where only the fixation point was visible. The structural MR image for each subject was segmented to obtain flat surface maps on which the retinotopic areas were mapped using the vertical and horizontal meridians defined by the scans.

Perceptual persistence

Subjects were presented with 3 different stimulus conditions (see Fig. 1 and http://www.med.uwo.ca/neuroscience/gap/demo/color.htm for a demonstration).

1) Move Stop: Segmented black-line drawings of objects were superimposed on a background of randomly oriented black lines (see Fig. 1A). When stationary, subjects confirmed that the objects were not distinguishable from the background and thus invisible before each scan. The segmented line drawings and background lines rotated in counter phase, clockwise and counterclockwise ±15°, with a period of 2.5 s. The rotating stimuli were presented for 12 s at which point the movement stopped and the combined background and object remained on the screen for another 12 s.

2) Color Stop: The same objects (black) were superimposed on a background of randomly oriented red lines. The red background lines differed from the black lines, thus defining the object in both hue and
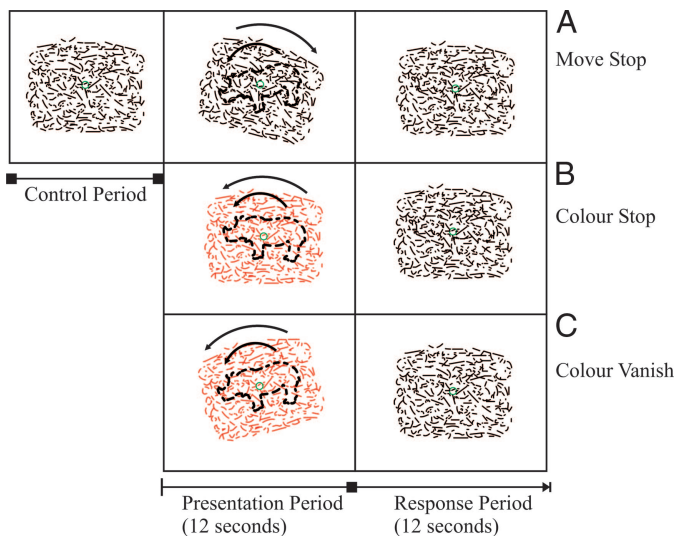
FIG. 1. Shape-persistence task. *A*: Move Stop condition: fragmented object (a rhinoceros, here depicted in a heavier black line for the purpose of illustration) and the background move in opposite directions to each other during the presentation epoch. In the response epoch, the object and the background stop moving. *B*: Color Stop condition: fragmented object appears in black and the background lines are red. Object and background move together during the presentation epoch. In the response epoch, the object and background stop moving and the background lines change to black. *C*: Color Vanish condition: presentation epoch is the same as the Color Stop conditions, but in the response epoch, the object is removed, the background stops moving, and the background lines are changed to black. Note: objects were drawn with thicker lines to make them visible in the figure only.

luminance (see Fig. 1*B*). The objects and the background rotated *together*, clockwise and counterclockwise ±15°, to prevent locally based color adaptation at the retinal level. Color adaptation was avoided because it could have produced artifactual persistence based on the continuing presence of a color aftereffect cue. The rotating stimuli were presented for 12 s at which point the movement stopped and simultaneously the background lines changed to black. The background lines and object remained on the screen for 12 s. The rationale for making the background change color rather than the object was to keep the visual attributes of the figure (black line fragments) the same across all 3 conditions.

3) Color Vanish: The same stimuli as those in Color Stop were presented, but after the movement stopped at 12 s, the object lines were removed and the background lines changed to black and remained on the screen for 12 s (Fig. 1*C*). We did not include a Move Vanish condition because behavioral pilot studies showed no differences between the Move Vanish and Color Vanish conditions. We opted to remove the "Move Vanish" condition in the interests of maximizing power for the fMRI experiment.

Perceptual persistence was measured by asking subjects to indicate with a button press when the percept of the object had disappeared. Using an event-related design, 4 functional scans were performed with 26 epochs per scan with each epoch lasting 12 s. The first and last epochs were control epochs in which only the background and fixation were presented. Epochs alternated between presentation of the stimuli with the motion or color cues present and a response epoch to measure persistence after motion or color/brightness cues had been removed. The Move Stop, Color Stop, and Color Vanish conditions were repeated 4 times in each of the 4 scans in a pseudo-random order such that no condition or image repeated more than twice in each scan.

Image analysis and regions of interest (ROIs)

Analysis was carried out using the Brainvoyager 4.9 software. 3D statistical maps were calculated for each subject based on a general

linear model. MT+ was defined as a set of contiguous voxels that showed significantly stronger activation ($P < 10^{-4}$) to moving versus stationary bars. LO was defined as a set of contiguous voxels, lying posterior to MT+, which showed significantly stronger activation ($P < 10^{-4}$) to intact versus scrambled objects. The retinotopic ROIs were localized using surface maps delineating the borders between V1, V2, VP, and V4v in each subject. The thresholds for the ROIs were also corrected for multiple comparisons ($P < 0.0001$ for LO and MT+ and $P < 0.05$ for the retinotopic areas). Because the perceptual persistence data were limited to 5 slices, the retinotopic ROIs were restricted to the lower half of the occipital lobe.

Perceptual persistence scans

For each perceptual persistence scan we extracted the fMRI response by averaging the data from all activated voxels within the predefined ROIs. The average percentage signal change for the 3 stimulus conditions (Color Vanish, Color Stop, Move Stop) was calculated using the last 12 volumes from the control epochs occurring at the beginning and end of each scan as baseline. We then averaged the signal time course across trials in each condition from each scan independently for each subject.

The persistence of brain activation was measured by calculating when the fMRI signal had decreased by 25% relative to the peak. To determine the time point of a 25% decrease in activation that was independent of the initial size of the response, the data were normalized to the average activation of 5 volumes before and after the removal of the binding cue (total, 10 volumes). Persistence was also measured by averaging the normalized fMRI responses between the time points 6 and 12 s after the binding cue was removed. This is the period when there was a possible divergence between the fMRI signal for the Color Vanish condition and the fMRI signals for the Color Stop and Move Stop conditions in all regions (Fig. 3, gray bar).

R E S U L T S

Behavioral data

A repeated-measures one-way ANOVA was performed with 3 levels (Color Vanish, Color Stop, and Move Stop) on the persistence latencies. A clear difference was found between the 3 stimulus conditions [$F(2,6) = 18.32$, $P = 0.0002$]. Figure 2 shows that the percept of the object lasted longer in the Color
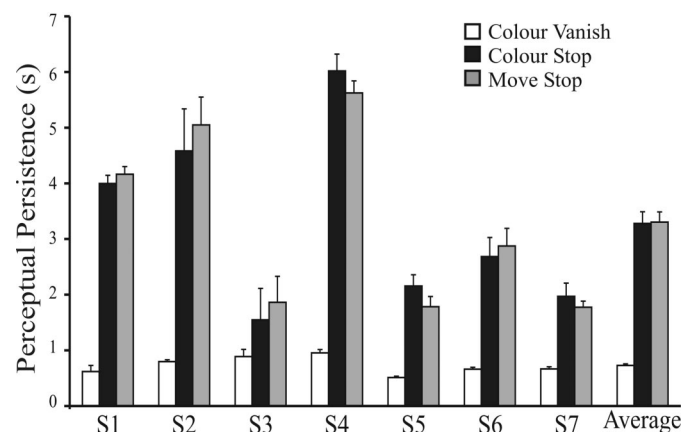

FIG. 2. Individual perceptual persistence (s). During the response period, subjects indicated with a button press when their subjective experience of an object was gone. Object persisted significantly longer when the local features remained (black, initial segregation by color/brightness; gray, initial segregation by motion) compared with when they vanished (white). Nature of the binding process (motion or color/brightness) had no influence on the length of persistence.

Stop (3,280 ms) and Move Stop conditions (3,304 ms) compared with the Color Vanish condition (729 ms). Post hoc comparisons (paired *t*-test, Bonferroni corrected, alpha = 0.016) confirmed that persistence lasted longer in the Color

Stop and Move Stop conditions and that there was no reliable difference between the Color Stop and the Move Stop conditions ($t < 1$).

fMRI Data

The normalized averaged time course of brain activation in the ROIs (LO, V1, V2, VP, V4v, and MT+) to the 3 stimulus conditions are shown in Fig. 3. In area LO the initial presentation of the stimulus, when the object can be separated from the background either by a motion cue or a color/brightness cue, caused an increase in activation. When the cues are removed, activation decreased most quickly in the Color Vanish condition (thick solid line), that is, the condition in which the entire object has been removed. In contrast, activation persisted for a while before returning to baseline when the cues (motion or color/brightness) were removed and the fragmented lines composing the object gradually merged with those of the background (Color Stop and Move Stop conditions). A comparison of the results from each of the ROIs shows that there was a gradual increase in persistence of brain activations through the cortical hierarchy. In contrast MT+ showed no persistence.

Two dependent measures were used to quantify the persistence of the activation. In the analysis of the duration of persistence (see Fig. 4*A*), we identified for each ROI the time (in seconds) when the fMRI signal first decreased by 25% of its normalized value (see METHODS). The 25% signal drop was calculated for each condition, in each hemisphere, independently for each subject. In the analysis of the magnitude of persistence (see Fig. 4*B*), we calculated the average fMRI signal on the normalized data between the time points of 6 and 12 s after the binding cue was removed across both hemisphere and condition. It is during this time period that the % fMRI signal change for the Color Vanish condition and that for the Color Stop and Move Stop conditions show the most divergence across all areas (see Fig. 3). In Fig. 4, *A* and *B* it can be seen that the greatest difference between the Move/Color Stop and Vanish conditions occurs in LO and V4v and that this follows a gradual increase in both the duration and magnitude of persistence in brain activation through the cortical hierarchy.

To quantify the increase in persistence of brain activations across the cortical hierarchy, a repeated-measures one-way ANOVA with 5 levels (V1, V2, VP, V4v, LO) was performed on the Color Stop and Move Stop conditions followed by a trend analysis using linear function contrasts (−2, −1, 0, 1, 2). In the Color Stop condition there were significant differences in the duration of persistence [$F(4,24) = 10.59, P < 0.0001$]
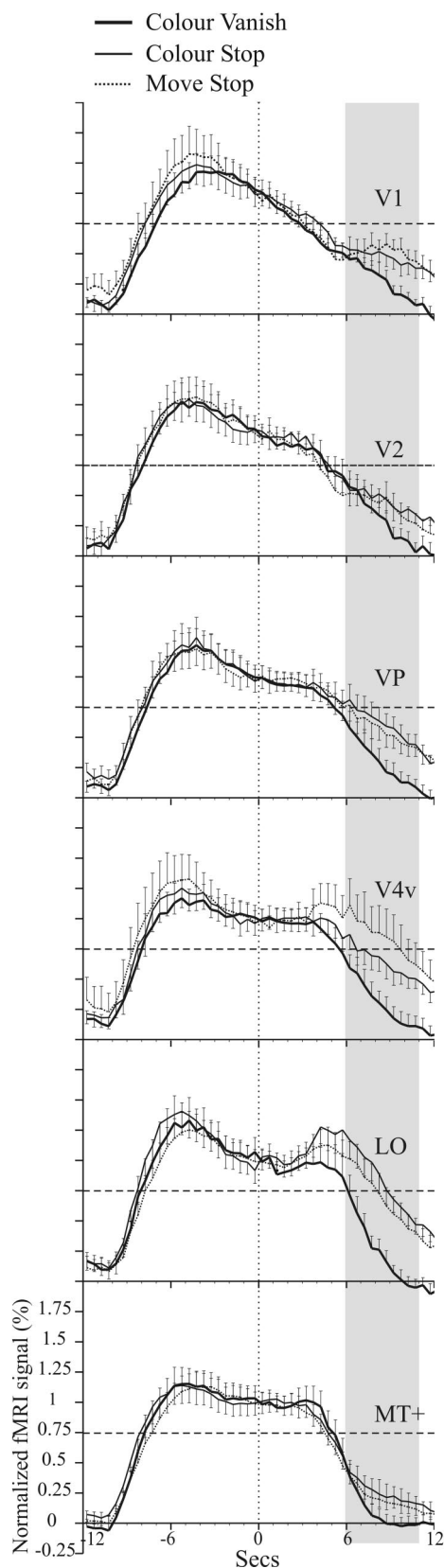

FIG. 3. Average time course of brain activation before and after the binding cues are removed. Normalized average time course of brain activation (*y*-axis) in the 7 subjects for the 3 stimulus conditions were plotted against time (s) in lateral occipital (LO), middle temporal (MT+), and retinotopic areas. Vertical dotted line indicates the period when the binding cues were removed. Dashed horizontal lines indicate the point at which the functionalized magnetic resonance imaging (fMRI) signal change decreased by 25%. Gray area indicates the time window in which persistence was measured. It is clear that there is greater persistence of brain activation during the period when the local features of the objects remained (thin solid line, initial segregation by color/brightness; dotted line, initial segregation by motion) compared with when they vanished (thick solid line). There is a gradual increase in the persistence of brain activations across the cortical hierarchy, which peaks in areas LO and V4v.
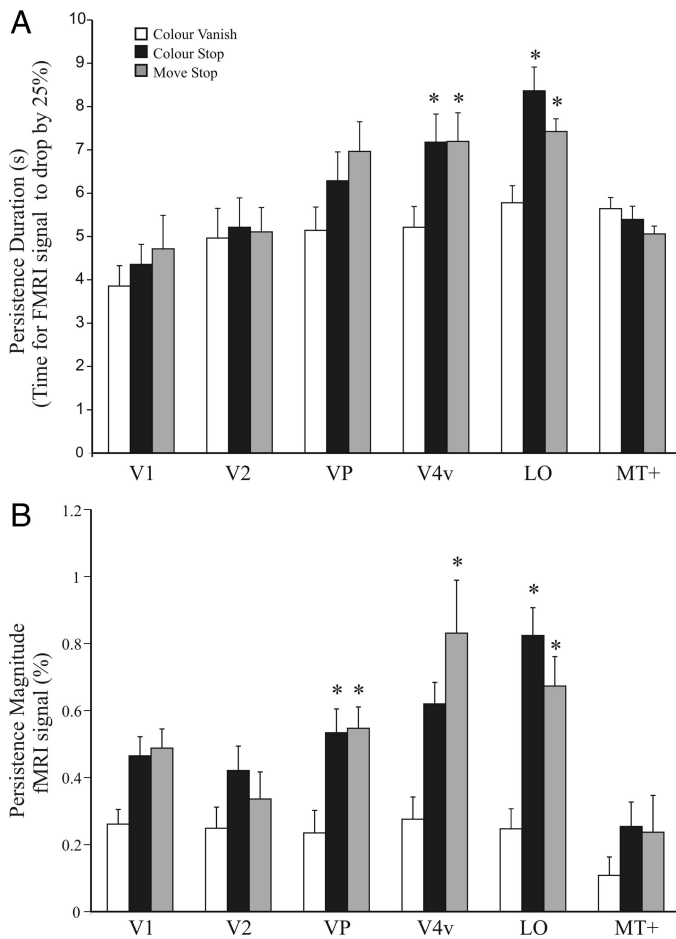
FIG. 4. Measures of persistence in brain activation in LO, MT+, and retinotopic areas. Persistence in the stop conditions (black, initial segregation by color/brightness; gray, initial segregation by motion) and the vanish condition (white). *A*: persistence duration measured as the time needed for the normalized fMRI signal to decrease by 25% of the peak intensity (*y*-axis). Signal drop of 25% was calculated for each condition in each hemisphere for each region of interest (ROI), independently for each subject and then averaged. *B*: persistence magnitude measured as the % of fMRI signal change (*y*-axis) averaged on normalized data during the persistence phase (6–12 s). Note that in both measures, persistence shows a gradual increase across the cortical hierarchy and peaks in areas V4v and LO. Significant differences between the Color Vanish condition and the Move Stop and/or the Color Stop conditions are marked with an asterisk.

and in the magnitude of persistence [$F_{(4,24)} = 8.03$, $P < 0.0001$] across these brain regions, which varied linearly as a function of the cortical hierarchy [Duration: $F_{(1,6)} = 22.47$, $P = .003$; Magnitude: $F_{(1,6)} = 19.72$, $P = 0.004$]. In the Move Stop condition there were significant differences in the duration of persistence across the cortical hierarchy [$F_{(4,24)} = 11.28$, $P = 0.01$] and the magnitude of persistence [$F_{(4,24)} = 2.99$, $P = 0.04$] and the duration of persistence showed a linear trend [$F_{(1,6)} = 39.46$, $P = 0.04$].

To assess differences between experimental conditions in each of the regions repeated-measures ANOVAs were performed on the data for each of the 6 regions with hemisphere (left/right) and stimulus conditions (Color Vanish, Color Stop, Move Stop) as within subject factors. Because there were no reliable differences between the right and left hemispheres, the data were collapsed across hemispheres and paired *t*-tests (Bonferroni corrected) were performed on the data from those

regions that showed significant ($P \leq 0.05$) differences between stimulus conditions in the repeated-measures ANOVA. For measures of the duration of persistence in brain activations, no reliable differences were found between the 3 stimulus conditions in areas V1, V2, and VP. In area MT+ a repeated-measures analysis on the duration of persistence showed a significant difference between stimulus conditions [$F_{(2,12)} = 3.895$, $P = 0.05$], although the more conservative Bonferroni comparisons between the 3 conditions were not significant. Consistent with the behavioral results, there were significant differences between conditions in areas LO [$F_{(2,12)} = 13.67$, $P = 0.0008$] and V4v [$F_{(2,12)} = 7.38$, $P = 0.008$]. Pairwise comparisons showed that brain activations persisted longer in both the Move Stop and Color Stop conditions compared with the Color Vanish condition in each of these regions (see Fig. 4*A*).

For measures of the magnitude of persistence, there were no reliable differences between conditions for areas V1, V2, and MT+. There were, however, significant differences between stimulus conditions, in areas VP [$F_{(2,12)} = 8.55$, $P = 0.005$], V4v [$F_{(2,12)} = 8.48$, $P = 0.005$], and LO [$F_{(2,12)} = 13.79$, $P < 0.001$]. As shown in Fig. 4*B* there were greater fMRI responses in the Color Stop and Move Stop conditions compared with the Color Vanish condition in these areas (confirmed by pairwise Bonferroni-corrected comparisons).

To examine the relationship between the fMRI activation and subjects' response to the disappearance of the objects in the Color Stop and Move Stop conditions a median split was performed on the fMRI data based on the speed of the associated behavioral responses. Each condition consisted of 4 trials per scan. The 4 trials were rank-ordered according to the behavioral persistence latencies and divided into 2 equal halves (short/long). This allowed us to compare the fMRI responses associated with longer-persistence latencies with those associated with shorter-persistence latencies. This analysis was performed on the fMRI data extracted from LO and MT+. A 2-way repeated-measures ANOVA with factors of Persistence (short/long) and Binding Cue (color/move) was performed on the data from LO, resulting in a main effect of Persistence [$F_{(1,6)} = 12.08$, $P = 0.01$]. From Fig. 5 it can be seen that longer-persistence latencies produced longer persistence in brain activation in both the Color Stop condition [$t_{(1,6)} = 2,78$, $P = 0.03$] and the Move Stop condition [$t_{(1,6)} = 4.08$, $P = 0.007$] for area LO. In contrast, there were no reliable differences in MT+. Longer persistence latencies did not produce more persistence in the fMRI response in MT+. For both analyses, there were no reliable differences between the Move Stop and Color Stop conditions.

In summary, persistence in brain activation lasted longer in the Color Stop and Move Stop conditions compared with the Color Vanish condition, similar to the behavioral results. The duration and magnitude of the persistence of brain activations increased gradually across the cortical hierarchy, peaking in the intermediate visual areas, V4v and LO. Interestingly, there were no reliable differences between the Color Stop and Move Stop conditions in either of the measures of persistence, suggesting that the persistence of brain activation is independent of whether the form was defined by color/brightness similarity or motion. In fact, Fig. 6 shows that the location of areas activated in the persistence phase (6–12 s after removal of binding cues) of the Color Stop condition overlapped consid-
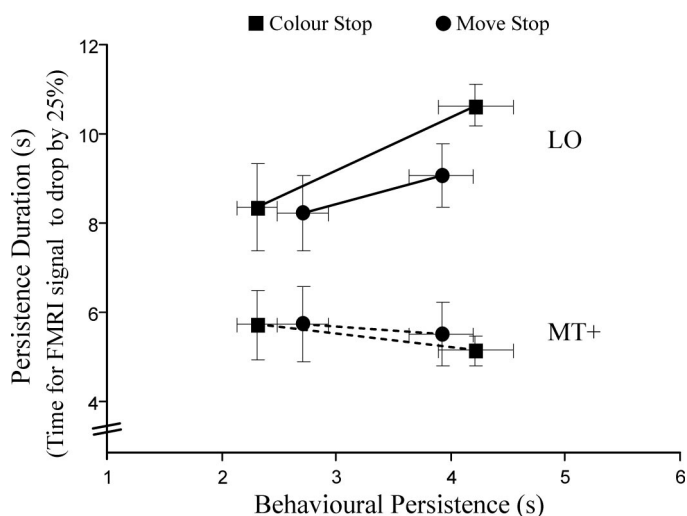
FIG. 5. Relationship between persistence latencies and persistence in brain activation. A median split was performed on the fMRI data based on speed of the behavioral responses. This allowed us to compare the fMRI responses associated with longer persistence latencies to those associated with shorter persistence latencies. Behavioral measure of persistence (*x*-axis) for motion (circle) and color (square) defined forms is plotted against the duration of persistence in brain activation (*y*-axis). Solid lines represent the persistence in brain activation found in LO and the dashed lines represent the persistence in brain activation found in MT+. Note that shorter persistence latencies are associated with shorter durations of persistence brain activation in LO, but in MT+ the amount of perceptual persistence does not vary as a function of the length of persistence shown in the behavioral measure.

erably with those activated in the persistence phase of the Move Stop condition. The averaged Talairach coordinates in each condition confirm the strong overlap between the 2 conditions in both LO and V4v (see Table 1). Student's *t*-tests were performed comparing the Talairach coordinates for the Move Stop and Color Stop conditions in LO and V4v and no reliable differences were found. This is a strong indicator that the mechanisms involved in maintaining the binding of visual elements into an object percept are independent of the cues that initiate the binding process.

DISCUSSION

Our findings suggest that the maintenance of integrated perceptual wholes is an emerging property within the ventral visual stream. Persistence in brain activation showed a gradual increase in duration across the cortical hierarchy, peaking in V4v and LO. A similar pattern was found in relation to the magnitude of the fMRI signal in response to the persistence of global percepts. Comparable to the findings of Ferber et al. (2003, 2005), there was no persistence of brain activation in area MT+, confirming their claim that MT+ is not involved in sustaining an integrated percept of the fragmented objects. In addition, we looked for differences in the effects of perceptual persistence contingent on whether visual elements were grouped into perceptual wholes on the basis of motion or on the basis of color/brightness cues. No differences were found between the persistence of brain activation to forms defined by motion and the persistence to forms defined by color/brightness in either LO or the earlier retinotopic regions. The results have important implications for the development of theories of perceptual memory and further our understanding of the neural correlates of perceptual continuity.

Magnusson and Greenlee (1999) claimed that early visual perceptual memory would be located early in the cortical stream, beyond V1, but before the formation of a structural description of an object. They also claimed that this system of perceptual memory involved parallel storage mechanisms dedicated to processing information from a single dimension. Based on this description of perceptual memory one could expect effects of perceptual persistence in the retinotopic areas V2, VP, and V4v as well as LO. Given that V4 is known to be involved in color perception (Bartels and Zeki 2000; McKeefy and Zeki 1997; Wade et al. 2002; Zeki et al. 1991) and, according to Magnusson and Greenlee (1999), color and motion signals are represented by separate memory systems, one might also expect stronger effects of perceptual persistence to color-defined forms compared with motion-defined forms in this area. In accordance with Magnusson and Greenlee's model of perceptual memory, we did see evidence of perceptual persistence in the lower visual areas; however, we did not find differences in either the levels of activation or the localization of activation related to the persistence of motion- or color-defined forms. In fact, we found that the brain regions activated in response to perceptual persistence for color-defined forms overlapped closely with regions activated in response to perceptual persistence for motion-defined forms.

The perceptual persistence found in this experiment may be related to the kind of perceptual persistence observed by Logothetis and colleagues in their experiments with reversible figures (Leopold et al. 2002; Maier et al. 2003). They found that reversible figures were stabilized when presented intermittently, interleaved with blank periods. That is, a perceptual state was maintained in the absence of a stimulus. Moreover, the interpretation of a reversible figure dictated the interpretation of subsequent figures. They also found that the stabilization of percepts was invariant to basic image transformations (e.g., color, size), suggesting that the influence of one percep-
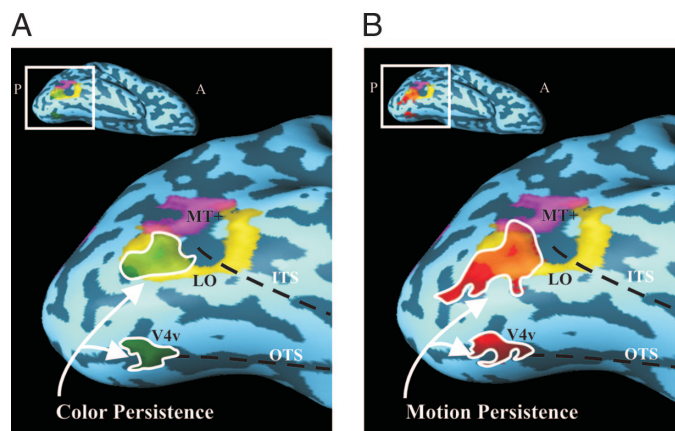

FIG. 6. Overlapping areas of persistence for motion and color. *A*: persistence activations for motion-defined forms (Move Stop, red) averaged across subjects. *B*: persistence activations for color/brightness defined forms (Color Stop, green) averaged across subjects. A comparison between the blood oxygenated level–dependent (BOLD) signals generated by the Move Stop and Color Stop conditions shows a remarkable degree of overlap. ROIs, averaged across subjects, were superimposed on inflated representations of the cortical surface. MT+ is depicted in pink, LO in yellow. Major sulci are labeled: ITS, inferior temporal sulcus; OTS, occipitotemporal sulcus. Persistence activations were generated by calculating the fMRI signal in the Color Vanish condition and subtracting it from the fMRI signal in the Color Stop or Move Stop conditions within the average persistence time period.

TABLE 1. *Talairach coordinates (n = 7)*

	Lateral Occipital (LO)			Vv4		
	x	*y*	*z*	*x*	*y*	*z*
Color Stop						
RH	40.57 ± 5.9	−65.71 ± 9	−7.14 ± 5.9	26.71 ± 9.2	−73 ± 3.1	−12.57 ± 6.5
LH	−44.71 ± 5	−71.43 ± 7.1	−3.57 ± 6.4	−30.43 ± 6.7	−73.43 ± 6.8	−14.57 ± 7.6
Move Stop						
RH	42.86 ± 5.8	−66.14 ± 7.1	−6.29 ± 4	27.86 ± 9.3	−71.71 ± 5.4	−12.43 ± 6.1
LH	−45.00 ± 5.1	−72.43 ± 8.6	−4.29 ± 6.1	−31.00 ± 6.2	−74.14 ± 8.2	−13.00 ± 8.9
Previous studies						
RH	41 ± 1.3	−68.1 ± 4.4	−9.1 ± 5.9	27 ± 4.7	−76 ± 8	−12 ± 5.9
LH	−43 ± 2.1	−69 ± 5.9	−6.6 ± 5.3	−26 ± 6	−76 ± 7.3	−13.5 ± 3.7

Values are means ± SD in mm. Source for LO coordinates (Grill-Spector 2003; Grill-Spector et al. 1998; Kourtzi et al. 2003; Lerner et al. 2002; Malach et al. 1995, 2002). Source for V4v coordinates (Bartels and Zeki 2000; Beauchamp et al. 1999; Hadjikhani et al. 1998; Kastner et al. 2000; McKeefry and Zeki 1997; Zeki et al. 1991).

tual state on a subsequent perceptual state was dissociated from basic perceptual attributes. Maier et al. (2003) speculated that the memory system involved in the stabilization of reversible figures was based on global representations and reflected the state of perceptual organization at a given time. This form of perceptual memory may be a subsystem of a more general perceptual memory system, the perceptual representational system (PRS), identified by Tulving and Schacter (1990).

Tulving and Schacter (1990) defined PRS as a preconcep-tual, nondeclarative form of memory, consisting of a number of subsystems that compute information about the global form and structure of visual objects. Based on evidence from per-ceptual priming experiments (Schacter 1990; Schacter et al. 1990, 1991; Tulving and Schacter 1990), they argued that PRS depends on encoding global structural descriptions of objects. It is improbable that the perceptual persistence we observed in our study is related to the encoding of structural descriptions of the objects. Ferber et al. (2005), using the same methods described in this study, found perceptual persistence to forms consisting of scrambled object fragments, which would have no appreciable 3D structure. Given Ferber et al.'s findings and our findings that perceptual persistence is independent of the binding cue (if our interpretation is correct) then perceptual persistence may rely on a form of perceptual memory that is intermediate to the early perceptual memory system outlined by Magnusson and Greenlee and that involving structural descriptions described by Tulving and Schacter. This implies that there are multiple levels of perceptual memory and that memory traces can be formed at any point during the construc-tion of an object representation.

The ability of higher visual areas to maintain global forms independent of the cues used to bind local features would be a useful property for maintaining stable percepts of objects in a nonstatic natural environment. Some caution is required, how-ever, before accepting this interpretation of the results. During the integration phase of the experimental trials, when the cues of motion or color were present, levels of activation for motion-defined forms were higher than those for color-defined forms in MT+ and LO. This suggests that the mechanisms involved in integrating local features into global shapes may not be independent of the cues used to bind them. The lack of differences in effects of persistence to motion- and color-defined forms may arise from limitations in the resolution of the fMRI signal. It is possible that the resolution is too coarse

to differentiate between subpopulations of neurons responding selectively to color- or motion-defined forms during the per-sistence phase of the trials. However, the resolution used in this study was sufficient to pick up differences in MT+ and LO during the integration phase of the trials. Also, Ferber et al.'s 2005 study showed that persistence occurred after motion was stopped and new object fragments (complements) were substi-tuted for fragments that were initially grouped together based on motion. Their results indicated that persistence was medi-ated by the formation of an object representation in which the contours were completed. In support of this claim, Lerner et al. (2002, 2004) demonstrated that LOC is involved in the com-pletion of object contours. They found greater activations to line drawings of objects that were obscured by a vertical grid compared with scrambled versions of the same stimuli. It thus seems reasonable to assume that if persistence is independent of the original object fragments, it is also independent of the cue that binds those fragments. Results of the study by Ferber et al. (2005) also have implications for the nature of the memory trace that subserves perceptual persistence. Much like the observations made by Maier et al. (2003), it would appear that the perceptual persistence detailed in this study is mediated by states of perceptual organization rather than by low-level–stimulus attributes.

Also of note, Mukamel et al. (2004) investigated the persis-tence of neural activation after a stimulus had been terminated. They presented stimuli at 2 rates, 1 and 4 Hz, and found that there was a nonlinear correlation between stimulus presenta-tion rate and the blood oxygenation level–dependent (BOLD) signal in higher visual areas, relative to retinotopic areas. That is, neuronal activation in higher-order visual areas persisted in the absence of a stimulus. Mukamel et al. suggested that the ability of neurons to maintain activity level in the absence of a stimulus might serve as a form of cortical short-term "iconic" memory. This ability of neural mechanisms in higher-order visual areas to sustain activity in the absence of a stimulus may link to our findings that perceptual persistence is most promi-nent in LO. However, it cannot fully account for the perceptual persistence we observed because this effect requires the object fragments to be physically present when the binding cue is removed. In addition, the duration of perceptual persistence when measured behaviorally was 2 s on average. This is out of the range for iconic memory (Phillips 1974). In fact, the Mukamel et al. experimental conditions most resemble our

Vanish condition in which the object fragments are removed when the binding cue is removed. We also see an increase in the time it takes for activation to decrease by 25% in LO relative to the retinotopic areas in the Vanish condition (see white bars in Fig. 4*A*).

Current neuroimaging and neurophysiological evidence posits roles for both lower and higher visual areas in the segregation of figure and ground (Altmann et al. 2003, 2004; Baylis and Driver 2001; Ferber et al. 2003; Kourtzi et al. 2003; Kourtzi and Kanwisher 2001; Murray et al. 2002; Roelfsema et al. 2002; Rossi et al. 2001; Rubin 2001; Smith et al. 2002; Stanley and Rubin 2003). In particular, Altman et al. (2003) and Kourtzi et al. (2003) demonstrated that the integration of local features into global shapes occurs at multiple sites in the retinotopic areas and LOC. They found no difference in levels of activation to global shapes across lower and higher visual areas. In contrast, we found evidence for a gradual increase in the persistence of activation across the cortical hierarchy. This suggests that the neural mechanisms involved in assembling a global shape from local features differ from those involved in maintaining an integrated representation once local features have been bound together. Altmann et al. (2003) and Kourtzi et al. (2003) speculated that activity in the lower visual areas in response to global shapes may be mediated by feedback connections from higher visual areas (see also Murray et al. 2002, 2004). Neurophysiological evidence supporting cortical feedback in visual areas is growing (Hupe et al. 1998; Lamme 1995; Lamme et al. 1998, 1999, 2002; Lee et al. 1998; Zipser et al. 1996) and a recent neural network model (Roelfsema et al. 2002) suggest that enhanced activity to global shapes found in lower visual areas is attributed to feedback from higher visual areas. Using a computational approach, Roelfsema et al. (2002) proposed that figure–ground segregation in the visual cortex requires different connection schemes that combine border detection and the grouping of figural regions. They argued that a feed-forward pathway through the cortical hierarchy is responsible for detecting the boundaries separating figural regions from background regions. The feedback pathway is responsible for grouping the figural region and is driven by neurons that respond maximally to the figure as a whole, and these neurons are located in high-level visual areas, most likely in the LOC. The flow of feedback is controlled by ensuring that only units modulated by feed-forward activity receive inputs by the feedback pathway.

Feedback may enhance the activity of neurons that respond to cues selective for grouping local features in a multiplicative manner, similar to that found in attention modulation (Kastner and Ungerleider 2000; Morrone et al. 2002; Treue 2001). In this study, persistence of brain activation is measured after the motion and brightness cues are removed. The removal of the cues disrupts the activity of neurons that were previously responding to specific properties of the visual elements (direction of motion or color). Thus the flow of feedback from higher visual areas is in turn disrupted, reducing effects of persistence in these lower areas. This may explain why there is gradual increase in persistence from lower to higher visual areas rather than an abrupt change. As information from the input image progresses through the cortical hierarchy, there is a gradual evolution from a cue-specific representation of features to a cue-independent representation of form. The influence of multiplicative feedback would become gradually weaker as one moved into foci that coded for cue-specific representations of features.

A possible interpretation of the effects of persistence is that the differences found between the "Vanish" and "Stop" conditions reflect the brain's response to stimuli that differ in the number of fragmented lines rather than the persistence of a global shape. Although this interpretation cannot be ruled out entirely with the current design, it is more likely that the persistence found in brain activation correlates with the participants' phenomenological experience of perceptual persistence for the following reasons. First a comparison of the brain activation produced by trials in which observers experienced longer or shorter perceptual persistence showed a difference. Longer-persistence latencies produced longer persistence in brain activations and shorter-persistence latencies produced shorter persistence for brain activations in area LO. In contrast, the same median split performed on the fMRI data in MT+ showed no differences in the persistence of brain activations associated with longer or shorter behavior-persistence latencies. Second, if the visual cortical areas responded to stimuli with a greater number of fragments rather than to a global form, then the activation should not decrease appreciably during the period (12 s) in which those fragments are present. However, the results show that activation in the Stop conditions drops toward baseline at approximately 7 s after the removal of the binding cue, in LO and the retinotopic areas. Third, there is no reason to assume that neurons with larger receptive fields will respond more strongly to stimuli with a greater number of fragmented lines than neurons with smaller receptive fields. We found a gradual increase in the degree of difference between the Stop and Vanish conditions across the cortical hierarchy.

To conclude, previous studies (Ferber et al. 2005; Kleinschmidt et al. 2002) demonstrated the involvement of LOC in the maintenance of a global percept. The present study establishes that the retention of a global percept is an emerging property of the ventral visual stream. Persistence in brain activation showed a gradual increase in duration and in the magnitude of the fMRI response across the cortical hierarchy, which peaked in V4v and LO. Because color and motion binding cues did not produce differential effects of persistence, we posited that perceptual persistence is mediated by a subsystem of perceptual memory that operates before the formation of structural descriptions of objects, but after early perceptual memory. This system may reflect the perceptual organization of visual stimuli. Furthermore, the time courses of activation we observed in LO and the retinotopic areas suggest that the neural mechanisms involved in assembling a global shape from local features differ from those involved in maintaining an integrated representation once local features have been bound together.

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