

The Neural Structures Expressing Perceptual Hysteresis in Visual Letter Recognition

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Summary

Perception can change nonlinearly with stimulus contrast, and perceptual threshold may depend on the direction of contrast change. Such hysteresis effects in neurometric functions provide a signature of perceptual awareness. We recorded brain activity with functional neuroimaging in observers exposed to gradual contrast changes of initially hidden visual stimuli. Lateral occipital, frontal, and parietal regions all displayed both transient activations and hysteresis that correlated with change and maintenance of a percept, respectively. Medial temporal activity did not follow perception but increased during hysteresis and showed transient deactivations during perceptual transitions. These findings identify a set of brain regions sensitive to visual awareness and suggest that medial temporal structures may provide backward signals that account for neural and, thereby, perceptual hysteresis.

Introduction

Perceiving objects in our physical environment is not an inevitable reflexive consequence of being confronted with a stimulus or directing attention. It can be formulated as a dynamic process of selecting and matching a sensory input to that predicted on the basis of higher-order representations (Tanaka, 1997; Logothetis, 1998; Treisman and Kanwisher, 1998). Perceptual awareness results from this constructive process, and it is essential to stabilize percepts against continuous and often critical shifts of low-level stimulus parameters, such as contrast levels, that occur at the level of the sensory receptors.

Here, we report a functional neuroimaging experiment with continuously drifting sensory input parameters that mediated nonlinear, categorical transitions of percep-

tual awareness (Figure 1). We generated perceptual hysteresis by slowly increasing the contrast of an initially hidden visual stimulus until the percept “popped out” and then reducing it again until the percept “dropped out.” Hysteresis refers to the fact that during contrast degradation, the drop out of the percept occurs at a lower contrast level than the one at which pop out occurs during contrast build-up. Hence, over a limited range of identical physical stimuli, the percept was absent in the case of increasing contrast and present in the case of decreasing contrast. This enabled us to assess brain activity as a function of perception, while the physical parameters of the sensory input were matched and only the history of stimulation (and perception) differed.

This experimental scenario disrupts stimulus-response coupling (i.e., a function that ideally locks the relationship between a stimulus and the neural response it engenders). We used perceptual hysteresis to define in which brain regions the emergence of a percept is associated with an additional response, over and above that accounted for by stimulation alone. We also sought brain structures that, while insensitive to a visual percept per se, selectively activate during perceptual hysteresis. Such a response would suggest a role in mediating a top-down influence that maintains a percept despite impoverished sensory input.

Results

Using functional magnetic resonance imaging (fMRI), we continuously recorded brain activity of human observers looking at a noisy visual stimulus field that contained the hidden shape of a letter (Figure 1; see Experimental Procedures). Gradually increasing the average luminance contrast (dot density in the figure relative to background) evoked perceptual pop out. During subsequent contrast reduction, perceptual awareness persisted in general down to and beyond this threshold, until perceptual drop out occurred. This cycle was immediately repeated within a scanning session so that pop out in the second run differed from the first by being primed. All perceptual transitions were reported by key presses (for behavioral data see Experimental Procedures).

This experimental design allows several analytical approaches. In a first step, we defined candidate areas for manifestation of neural hysteresis by delineating brain regions sensitive to the sustained presence of a percept (see Experimental Procedures). Greater activity during a percept was generally right lateralized and occurred in ventral lateral occipital, inferior parietal, premotor, and inferior prefrontal cortices, but not in early visual areas (Figure 2). The time course of fMRI signal change in these areas revealed that activity was greater during intermediate than frankly supra-threshold stimulus contrast (“M” shaped configuration) and that it was greater during the first run with a percept (as confirmed by contrasting the related images of the first and the immediately ensuing second runs with the same letter). This response modulation in percept-sensitive areas during

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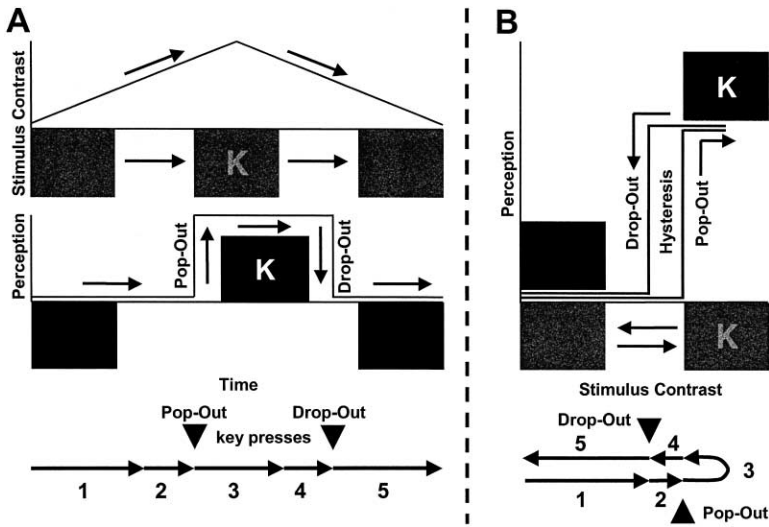


Figure 1. Experimental Design Generating Visual Perceptual Hysteresis

(A) If a shape (such as a letter) is contrasted relative to background by slowly increasing dot density (as in Figure 1), pop out from the background as a percept of the letter will often occur relatively late in the naive observer. Conversely, reducing contrast from a supra-threshold level and progressively degrading the stimulus engenders a perceptual drop out (i.e., loss of percept). This often occurs at a lower contrast threshold than that required for pop out during contrast increases. Hence, a linear stimulus change (top) translates into a nonlinear perceptual time course (bottom). (B) Plotting perceptual level as a function of contrast and direction of contrast change may reveal a hysteresis effect on visual awareness with respect to the experimentally controlled parameter of stimulus contrast. This phenomenon is used to dissociate perceptually driven brain activity from purely sensory stimulus-related activity. Numbered

arrows below both graphs indicate experimental conditions defined by subjects' key presses (large vertical arrowheads) at perceptual pop out and drop out. The presentation in (B) illustrates how the timing of drop out also served to define the contrast level at which epoch 2 begins and the timing of pop out served to define the contrast level at which epoch 4 begins (see the section on Imaging Data Analysis in Experimental Procedures for more details).

a primed second run is in line with the findings of others (Buckner et al., 1998; Grill-Spector et al., 1999; Büchel et al., 1999; Henson et al., 2000; James et al., 2000).

The opposite comparison—probing greater responses during the primed second, as opposed to the first percept—showed activation in both medial temporal cortices (Figure 2B). Although activity of the medial temporal cortex did not correlate with the presence of a percept per se, it increased following the first pop out and remained elevated throughout the remainder of the session, demonstrating only transient decreases at perceptual transitions (as confirmed in trial-by-trial event-related analyses of all the pop outs and drop outs).

In the next step, we confined our analysis to the first run i.e., the run in which perceptual hysteresis occurred, and compared brain activity during increasing and decreasing stimulus contrast. We plotted MRI signal intensity as a function of stimulus contrast (instead of experimental time) by folding activity during stimulus degradation back onto activity during stimulus build-up (Figure 3; see also Figure 1). We used the behavioral data to individually identify trials in which perceptual hysteresis occurred (i.e., at least two contrast steps separated pop out and drop out). These were analyzed separately from trials in which pop out and drop out occurred at similar contrast levels (less than two contrast steps of difference). This procedure had the advantage of ensuring that any hysteresis in the fMRI data could not be interpreted as an effect of hemodynamic latency or responses of single voxels (e.g., from draining veins). Since these possible confounding factors were constant across trials, hysteresis in the fMRI time course data that correlated with perceptual hysteresis could be confidently related to differential neural activity between such trials.

Significant hysteresis effects were observed in the fMRI time course data in all of the percept-sensitive areas but were not seen in trials without perceptual hysteresis (Figure 3). An exception to this general behav-

ior was found in lateral occipital cortex: due to the characteristic response adaptation found in this area, there was a decay of activity after pop out. In perceptually negative trials, this manifested as a reverse hysteresis (i.e., greater activity during contrast build-up than during degradation). In trials with perceptual hysteresis, the fMRI signal during the phase of degrading contrast was greater than compared to those without. This hysteresis-related phenomenon effectively reversed the adaptation-associated deactivation. Consequently, activity in trials with perceptual hysteresis reached similar levels with both increasing and degrading contrast, but this neural hysteresis effect was not large enough to produce a net activation in these trials because of attenuation by adaptation effects (Figure 3). Hence, evidence for neural hysteresis in this area remains indirect.

In trial-by-trial event-related analyses, we confirmed that all of the percept-sensitive areas showed transient activations linked to the individual timing of pop out and drop out across trials. This result suggests that sustained activation in these areas between pop out and drop out was related to the duration of the percept in each trial. While psychophysical experiments have pointed to both qualitative and quantitative differences in the attentional consequences of object appearance and disappearance (Samuel and Weiner, 2001), we found the same qualitative (spatial) event-related response pattern for both pop out and drop out. There was, however, a quantitative difference in that responses to pop out were significantly greater than those to drop out ($p < 0.001$) in all percept-sensitive areas, in line with the notion that object appearance is a more salient perceptual event than disappearance.

Given the presence of event-related activations at times of perceptual change (both pop out and drop out), the hysteresis appearing in the average activity plots in Figure 3 could result from a temporal smearing of event-related responses to jittered drop outs which, in trials with perceptual hysteresis, occur at lower contrast lev-

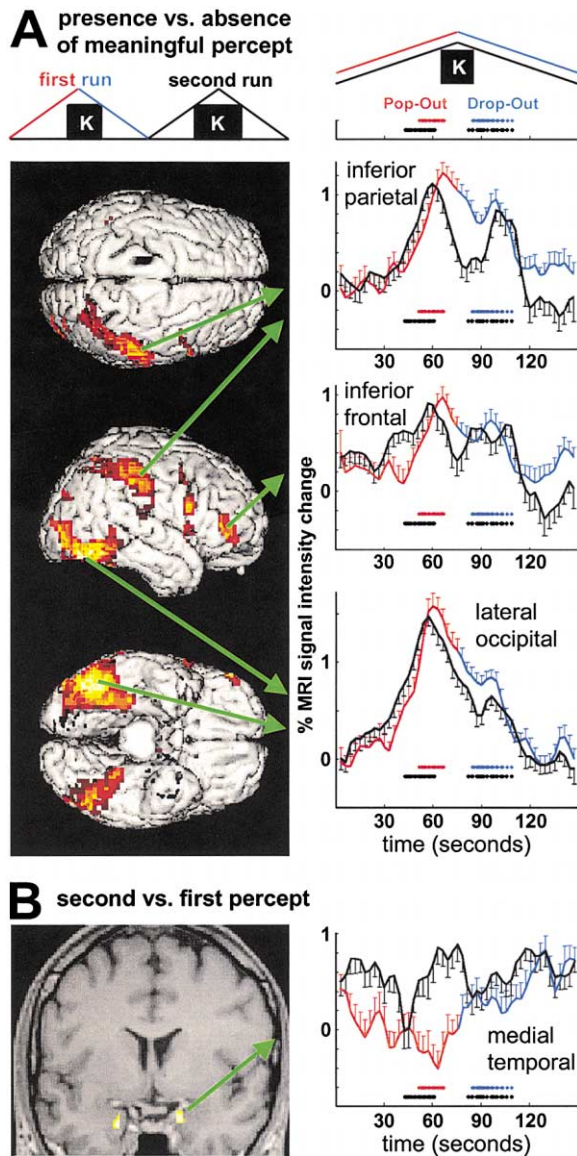


Figure 2. Percept-Sensitive Brain Areas and Their Activity Time Courses

(A) Brain areas activated by the presence of a visual percept. During two runs of stimulus build-up and degradation (in the insert, the red line indicates stimulus build-up, the blue line indicates degradation in the first run, and the black line indicates the second run), subjects report the pop out and drop out of the visual percept (e.g., letter “K” in the insert). Areas color-coded and superimposed onto template brain renderings underneath show activity time courses significantly correlated with this perceptual regressor ($p < 0.05$, corrected). The fMRI signal intensity time courses in these areas for both the first (red/blue) and second (black) runs within a given session are superimposed on the right for the local maxima, indicated by green arrows on the left. These are pooled and normalized grand average data from 40 sessions in 6 subjects with one-sided error bars. Dots with the corresponding color-coding indicate the timing of pop out and drop out events in the first and second runs. Note overall perceptual hysteresis in the first, but not the second, run during which activity rises earlier but remains lower.

(B) Brain areas with greater activity when the same percept is evoked for the second time. This statistical comparison ($p < 0.05$, corrected) reveals bilateral medial temporal cortex activation, as shown by superimposition onto a coronal slice of the structural scan of one of the subjects. The underlying signal intensity time course with one-sided error bars is displayed on the right.

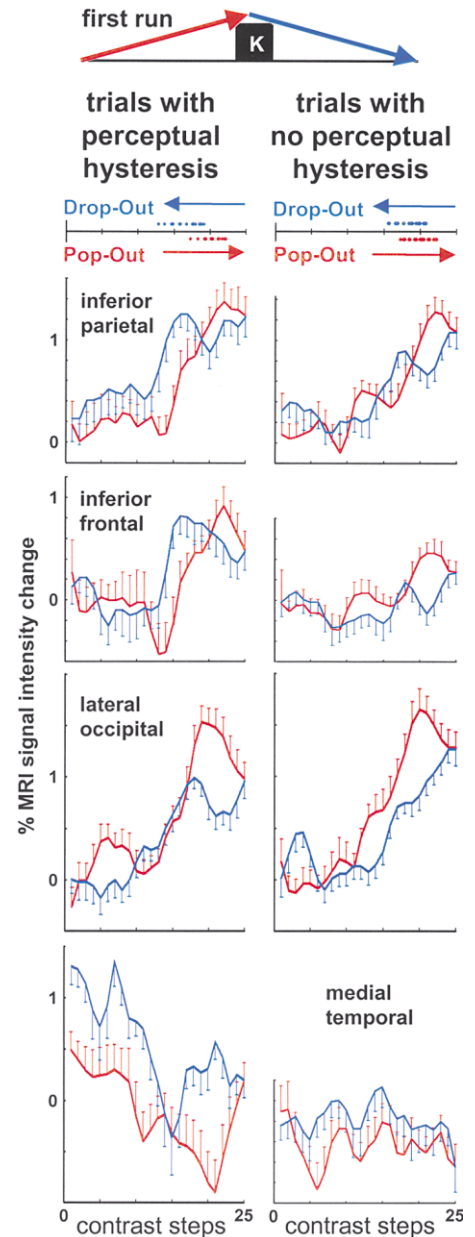


Figure 3. Hysteresis in Stimulus-Response Functions

The time course data of the first run from regions defined in Figure 2 were split into two groups, according to the presence (left) or absence (right) of perceptual hysteresis. Data are plotted with one-sided error bars as a function of stimulus contrast, wrapping back the activity time course during stimulus degradation (blue) onto activity during stimulus build-up (red). Each contrast step was presented for 3 s. The data come from the maxima of the respective foci defined in Figure 2 by contrasts probing percept-sensitivity (Figure 2 A) and enhanced activity during the second, as compared to the first percept (Figure 2 B), respectively. Individual pop out (red) and drop out (blue) events in the trials are indicated by dots displayed below the top insert.

els. In a final analysis performed only in perceptually positive trials, we focused on activity levels corresponding to the actual time for which subjects experienced hysteresis, as defined by trial-by-trial behavioral reports (see Experimental Procedures). We analyzed the activity related to the periods preceding pop out and drop out

(conditions 2 and 4 in Figure 1), but not those following them because they might be contaminated by the event-related responses (vertical arrowheads in Figure 1).

The results from this analysis confirmed that activity in percept-sensitive areas in inferior parietal, premotor, and prefrontal cortex shown in Figure 2 was significantly ($p < 0.05$) greater when identical physical stimuli evoked a meaningful percept than when they did not. Again, lateral occipital cortex did not show this pattern for the reasons detailed above. In addition to hysteresis in percept-sensitive brain areas, this analysis also revealed bilateral activation of the same medial temporal regions identified in comparisons between runs with identical stimuli (see above and Figure 2B). Thus, not only were they more active during the second run (as opposed to the first run with the same percept), but they were also more active within the first run when a percept was maintained during contrast degradation, compared to identical visual stimulation during contrast build-up that preceded the pop out.

Together, our findings suggest that a meaningful percept is associated with enhanced neural activity in a distributed set of associative visual and higher-order brain structures. The neural hysteresis effects we observed are not accounted for by physical stimulus properties (such as contrast level or frame length) because these were identical in the hysteresis range. A remaining problem is that when perceptual hysteresis occurs, the reports of pop out and drop out by key presses occur at systematically differing contrast steps. Conceivably, the act of reporting could have an influence on visual processing, for instance, through response-related contributions to activations in areas such as parietal and frontal cortex.

We therefore ran a second experiment with the same stimuli on three subjects who were only passively viewing and not required to produce behavioral reports. For analysis, we used an average of the behavioral data obtained from the subjects in the main study. This approximation proved adequate, since we found a very similar spatial distribution of signal changes that correlated with the time course of perception in the main study (Figure 4). When analyzing activity in these areas as a function of stimulus contrast, we found somewhat less-pronounced peaks close to the times of inferred perceptual change but again observed a clear-cut hysteresis effect (Figure 4). That this activity enhancement correlates with perceptual awareness remains an inference, but it cannot be related to an active execution of a task. Interestingly, in this experimental setting, pooled data showed a clear hysteresis effect in ventral lateral occipital cortex activity. This result suggests that both the adaptation of lateral occipital responses we saw with repeated stimulus presentations in our main experiment and occluded hysteresis were at least partially driven by the instruction to report perceptual transitions. This interpretation is compatible with previous demonstrations of instructed attentional modulation and response adaptation of ventral lateral occipital cortex activity (Desimone, 1996; Buckner et al., 1998; Grill-Spector et al., 1999; Büchel et al., 1999; Henson et al., 2000; James et al., 2000).

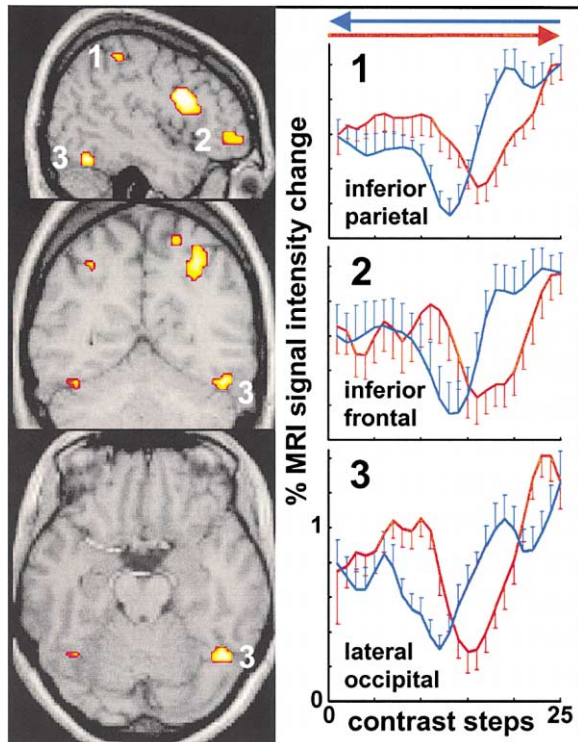


Figure 4. Hysteresis during Passive Viewing

The fMRI time series of three subjects was analyzed using the average perceptual boxcar function from the six subjects analyzed for Figures 2 and 3. Areas presumed on this basis to be percept sensitive ($p < 0.001$, uncorrected) are shown in the left-hand panels by superimposition onto a sagittal, coronal, and transverse section of the structural scan of one subject. The spatial pattern of these inferred foci is in excellent agreement with that displayed in Figure 2 for overt (reported) perceptual sensitivity. Numbering indicates corresponding foci, and the activity time courses in them (along with one-sided error bars) are displayed in the right-hand panel using the same color-coding as in Figure 3. Note hysteresis effects at similar contrast levels to those in Figure 3 across all three regions.

Discussion

Perceptual hysteresis was recognized by psychologists of the Gestalt school (Sekuler, 1996). It can be generated by mathematical models of perception that are based on psychophysical observations (Kelso, 1995), but the underlying neural processes are not understood. In this study, we used a visual paradigm that can elicit perceptual hysteresis, and we found that if, and only if, this happened, neural hysteresis occurred in a distributed network comprising several distinct brain structures. Hysteresis was used to dissociate neural activity related to explicit perception, and awareness from the activity related to physical stimulus properties.

Some components of the distributed responses we found may reflect the use of letters as visual object category (Solomon and Pelli, 1994; Polk and Farah, 1998) and low-frequency luminance patterning as contrast source. Activation in the ventral visual-associative areas reported here was found to be cue-independent in other studies (Grill-Spector et al., 1998; Kourtzi and Kanwisher, 2000), but the role of object categories is

more difficult to assess. In a positron emission tomography study, Dolan et al. (1997) used unrecognizable degraded pictures that became recognizable once they were presented with undegraded versions. Comparing blood flow responses to the two repetitions of identical stimuli, they found greater activity once the pictures were recognized in ventral visual areas specific to the visual category of the pictures (objects versus faces). They also reported medial and lateral parietal activations in response to recognition that were common to both categories. Our findings of hysteresis in the first trial and of earlier responses in the second (primed) trial are compatible with this report. In our experiment, differential brain activity as a function of perception was evoked by dynamic fluctuations in stimulus properties, but we used only one category of visual object. Yet, the localization of responses in ventral visual cortex we observed is compatible with results from studies that explicitly address the processing of single letters (Gauthier et al., 2000, comparing with faces). Studies comparing letter strings with digit and shape strings found additional anterior fusiform letter-specific foci (Polk et al., 2002).

Beyond the issue of category-specific representations in ventral visual cortex, both the localization of the other percept-sensitive areas we found and the presence of hysteresis effects in them is in good agreement with a body of experimental literature that has addressed the relation of perceptual awareness to patterns of distributed brain activity (Rees, 2001). These studies imply that perceptual awareness may, at least in part, share neural substrates with sensory input processing, attentional selection, and working memory (Courtney et al., 1997; Rees et al., 1997; Rees and Lavie, 2001). The effects of these cognitive functions on neural activity are not confined to single areas but are differentially weighted on regions constituting a distributed system. This formulation agrees with the observation that lesions at different locations may result in different neuropsychological deficits. Syndromes with profoundly different clinical phenomenology e.g., expressing predominantly attentional (neglect) or explicit perceptual disorders (agnosias), share the common feature of an uncoupling of (implicit) perception and awareness (Farah and Feinberg, 1997). This suggests that the emergence of perceptual awareness has a composite, rather than a unitary, cognitive correlate and a distributed, rather than a localized, neural correlate. In our experiment, hysteresis (i.e., activation during prolonged maintenance of a percept in spite of degradation of the stimulus) corresponds conceptually to a neural signature of visual awareness, rather than of other specific contributing cognitive functions. It is, therefore, not surprising that we found hysteresis effects distributed across a number of regions, including predominantly right-sided inferior parietal, premotor, and inferior frontal cortices. This finding supports the idea that multiple cognitive functions beyond input processing are involved in sensory awareness.

More complex functional response properties were found in the ventral lateral occipital cortex. The so-called lateral occipital complex (LOC) has been implicated in perception because it maintains its response to visual objects across contrast manipulations that remain in the perceptual range (Malach et al., 1995). Our approach here is orthogonal because we compared activity under

identical contrast conditions to show that a successful perceptual interpretation of a sensory input is accompanied by enhanced activity in this area (Figures 3 and 4). This percept-related activation is particularly noteworthy in LOC because one of its prominent response properties is adaptation (i.e., a reduction of response with stimulus repetitions). This LOC response property occurs not only with trains of identical stimuli, but also with trains of stimuli which, despite constant perceptual meaning (invariance), differ in physical properties such as size and position (Grill-Spector et al., 1999; Kourtzi and Kanwisher, 2000). Accordingly, response adaptation in LOC can be observed in our experiment following pop out, even though stimulus properties change continuously. While adaptation is already manifest in trials without hysteresis, our findings in trials with perceptual hysteresis show a relative activity increase in LOC that counterbalances adaptation. This enhanced signal parallels prolonged percept maintenance and suggests that activity in LOC is also modulated by visual perceptual awareness.

Further evidence in favor of a critical role of LOC in visual awareness is that LOC activity (fMRI signal) in response to blocks of brief masked presentations (20–500 ms) shows the highest correlation with visual recognition performance. Also, if for a given presentation duration recognition is improved by training, enhanced fMRI responses are recorded in LOC (Grill-Spector et al., 2000). A more recent fMRI study analyzed event-related responses to briefly presented and masked visual objects and found a relationship between explicit recognition and activity in LOC, as well as in an anterior region of the fusiform gyrus (Bar et al., 2001). The authors also showed an anterior progression of these responses along ventral temporal cortex as a function of the operationally defined level of recognition success.

While all of these studies addressed a direct relationship between amplitudes of LOC responses and recognition success, a study by James et al. (2000) investigated differences in the temporal pattern of activity levels immediately preceding and following recognition, as a function of priming. They used a gradual unmasking technique similar to that used in our study (i.e., with periods of stimulus build-up in the first and [primed] second trials). Responses to the types of visual objects under investigation in that study were found in frontal, parietal, and peristriate cortex and, most prominently, in the LOC. Responses in all foci showed response adaptation. The main finding was that, after priming, recognition occurred at lower contrast levels and that associated responses were thus evoked earlier but reached the same peak value. Additionally, however, differences in polynomial fits of the data with positive third-order coefficients for the primed, but not the nonprimed, trials suggested that the timing of peak activation for primed trials was shifted to the precognition period of the response. This finding was significant in LOC and posterior parietal cortex.

The three aforementioned studies (Grill-Spector et al., 2000; Bar et al., 2001, and James et al., 2000) differ from ours in several important ways. (1) They used rich composite stimuli that could be recognized in a gradual way, reflecting multiple successful recognitions at the component level. We attempted to minimize the impor-

tance of processing at a subcategorical level by using visual letters (i.e., stimuli that are not themselves composed of other meaningful percepts). (2) They used brief and masked presentations or gradual presentation to focus on activity at or close to the time of recognition (i.e., the onset of a percept). In our study, we used slowly waxing and waning stimulus contrast to address pop out and the ensuing presence of a percept separately, identifying associated activity by transient and sustained regressor shapes, respectively. Hysteresis was relatively short in relation to hemodynamic latencies, and it is, therefore, important to realize that the associated sustained activity was not only modeled differently, but also occurred with a different timing than the activations related to perceptual change. The epochs over which hysteresis was observed (conditions 2 and 4 in Figure 1) precede transient activations related to pop out and drop out (vertical arrowheads in Figure 1).

Although separated analytically, our results show that both transient responses to perceptual changes and sustained responses to perceptual awareness occurred in largely overlapping areas. In our setting, an initial transient component of a sustained response to a percept cannot be distinguished from a purely transient response related to the instant of pop out or recognition. Indeed, neuroimaging studies of perceptual rivalry during constant but perceptually bistable visual stimulation have shown both transient (i.e., switch-related) and sustained (i.e., percept-related) activations after perceptual transitions in ventral temporal visual areas (Kleinschmidt et al., 1998; Lumer et al., 1998; Tong et al., 1998). Furthermore, the frontoparietal structures showing transient activations during perceptual transitions in those studies (Kleinschmidt et al., 1998; Lumer et al., 1998) are largely congruent with those expressing hysteresis in this study.

How can these colocalized transient and sustained responses be related to the neural processes underlying visual perception? If framed in terms of “generative models” and, in particular, “predictive coding” models (Hinton and Ghahramani, 1997; Rao and Ballard, 1999), associative cortical areas may function by matching inputs received by lower cortical stations with a top-down signal that attempts to predict this input. In this formulation, it is inferred that patterns of neural activity fall into one of two classes. First, activity can be elevated during the interval between the onset of a percept and its disappearance. This sustained activity represents a successful perceptual interpretation (i.e., the joint presence of a sensory input and a matching signal, corresponding to a high-level representation). By virtue of the hysteresis effect we were able to delay and thereby dissociate the activity related to sustained perceptual awareness from the activity related to the sensory input. The second pattern of activity reflects the error or mismatch between bottom-up sensory information and top-down predictive signals. This will be greatest close to times of perceptual transition (i.e., from no letter to letter, and from letter to no letter). The resulting pattern of activity should exhibit two peaks coincident with perceptual pop out and drop out, a pattern we found in brain regions that we determined to be percept-sensitive. According to predictive coding theory, both patterns would characterize areas that integrate sensory input and prediction.

The aforementioned neuroimaging findings and theoretical considerations converge to identify brain structures involved in visual object perception from their functional behavior. Yet, the more fundamental issue is whether local computations in these structures fully account for perceptual synthesis. Both theoretical models (Carpenter and Grossberg, 1993; Ullman, 1995) and studies in nonhuman primates (Miyashita et al., 1996; Naya et al., 2001) suggest that perceptually successful processing of sensory input in visual association areas could depend on signals received from higher-order structures.

But how would activity in these higher-order structures change over time in our experimental setting? If formulated according to predictive coding, the computational aim of a structure providing a top-down signal would be to minimize error registered in lower visual processing areas by providing them with progressively refined predictions. Again, activity should then follow two patterns. If it reflects the matching of perceptual or mnemonic representations against incoming sensory input, it should transiently collapse once pop out is achieved by supra-threshold sensory input, signaling selection of a particular representation. Such a collapse should also occur when, during contrast degradation, percept stabilization by a top-down signal inevitably sooner or later fails, thus inducing perceptual drop out. In addition to this pattern of transient decreases related to perceptual changes, a sustained activity pattern will express a memory signal for perceptual processing. Associated activity should increase once a specific representation is evoked by a supra-threshold sensory input and persist in the face of subsequent successive degradation of that input. Such a persisting memory trace could even carry over into the second run and account for priming of perceptual pop out. The activity time courses we observed in the medial temporal lobe (and only there) are in accordance with both of these patterns (i.e., transient deactivations during perceptual changes) (Figure 2B) and sustained activation during hysteresis (Figure 3), as well as a carryover into the second cycle with the same stimulus (Figure 2B).

If tentatively interpreted this way, our findings provide a further illustration of how visual object recognition involves an interplay between ventral temporal cortex and the medial temporal lobe system (Tanaka, 1997). If perceptual awareness relies on the interaction of a top-down signal with sensory input in visual association areas, one would predict the top-down signal to delay, but not indefinitely prevent drop out, thus yielding the hysteresis we observed in stimulus-response functions of percept-sensitive areas. This speculative interpretation of our findings in medial temporal cortex is in accordance with theoretical models (Gluck and Myers, 1993) and also with other recent neuroimaging findings. Portas et al. (2000) found persistent activation in medial temporal and dorsolateral inferior frontal structures during percept maintenance, and Ranganath and D’Esposito (2001) described sustained medial temporal activation during maintenance of information no longer supported by sensory input. Most importantly, this interpretation is compatible with longstanding human and nonhuman primate studies relating visual recognition memory to basal medial temporal cortex (Scoville and Milner, 1957;

Zola-Morgan et al., 1994; Buckley and Gaffan, 1998; Brown and Xiang, 1998; Murray and Bussey, 1999; Brown and Aggleton, 2001).

In conclusion, our experimental setup using perceptual hysteresis elucidates distributed brain mechanisms underpinning visual perceptual synthesis and thereby contributes to an understanding of functional (computational) and structural (neural) models of recognition, perception, and phenomenal awareness. We found a set of brain structures in temporal, parietal, and frontal cortex that expressed in their response functions a hysteresis that correlated with perceptual hysteresis and did not depend on behavioral reporting. The spatial distribution of these effects is congruent with the regional functional properties derived from other activation studies. We identified a response pattern in medial temporal cortex that may correspond to a top-down signal that is relevant for recognition of a visual object and for maintenance of such a percept when the underlying physical stimulus is degraded toward subrecognition threshold levels. We therefore speculate that the medial temporal system is a candidate structure for the generation of prolonged activations in visual associative areas that may account for perceptual hysteresis.

Experimental Procedures

Subjects and Imaging

Data from nine healthy subjects (written informed consent; four females and five males with normal vision, in the age range of 22–36 yr) were acquired on a 2T magnetic resonance imager (Siemens Vision, Erlangen, head coil), obtaining a structural (T1 weighted) scan and series of blood-oxygenation-sensitive (T2* weighted) echoplanar image volumes every 3 s (32 adjacent oblique transverse slices, voxel size = $3 \times 3 \times 3$ mm³).

Experimental Paradigm

Prior to each scanning series (105 image volumes), subjects started looking at a field of random dots with a central fixation point, covering approximately $15^\circ \times 10^\circ$ of the visual field horizontally and vertically, respectively. In this background field of 640×480 pixels, every tenth pixel was a white dot, and the others were black. With the onset of scanning, a constant but randomized fraction of these dots (20%) were replaced with each scan volume. Additionally, dot density increased step-wise within a mask defining a letter by incrementing dot occurrence in 0.4 steps (i.e., every 10th, then every 9.6th, then every 9.2nd dot being white, etc. and applying the same 20% refresh rate with each frame as in the background). Both background and mask were subdivided into smaller fields into which randomization was constrained, yielding smoother luminance distributions and thus avoiding spurious dot agglomerations. For each of the four to eight sessions per subject, a different letter mask, position, and size were chosen, although all masks covered the central fixation point. Absolute vertical extent of the letters ranged from 180 to 240 pixels, corresponding to a height of approximately 3.5° to 5° visual angle. At far supra-threshold levels for letter recognition (i.e., subtotal accumulation of dots within the mask), the direction of contrast change was reversed, yielding a gradual decrease of dot density within the mask down to background (Figure 1). This run was immediately repeated a second time during ongoing scanning (i.e., during each fMRI time series a different letter stimulus was built up and degraded twice). In the first study, six subjects performed right hand key presses to indicate perceptual pop out and drop out in both runs. In the second study with three subjects, no behavioral reports were required. In both studies, subjects were instructed to maintain fixation on a central red point throughout scanning.

Behavioral Data

On average, subjects from the first experiment (with key presses) reported perceptual transitions at the 19th contrast step during the

first run and at the 18th contrast step during the second run, with standard deviations for each of these four event types (pop out and drop out in first and second run, respectively) ranging from 1.4 to 2.3 contrast steps. Pooling all trials, hysteresis (i.e., the difference in contrast step for pop out versus drop out in the first run) was barely significant ($p = 0.027$), even though in single trials, it could be as pronounced as 15s. The priming-related difference between contrast levels for pop out in the first and second run was clear-cut (one-sided *t* tests at $p < 0.05$). No significant hysteresis occurred during the second run. By splitting the trials into two groups on the basis of the occurrence of perceptual hysteresis of at least 6 s during the first run, the hysteresis effect for perceptually positive trials (18) became highly significant ($p < 0.000$), and no significant difference was found in the remaining perceptually negative trials (22). These groups represent the separate imaging data sets used for analyses (see Figure 3).

Imaging Data Analysis

For spatial processing and analysis, we used statistical parametric mapping (SPM, <http://www.fil.ion.ucl.ac.uk/spm>). In summary, all volumes were realigned, motion corrected, coregistered with the subjects' own structural MRIs, normalized into standard stereotactic space (template provided courtesy of the Montreal Neurological Institute), and smoothed using a 9 mm full-width at half maximum Gaussian kernel.

The data were analyzed by modeling hemodynamic responses that correlated categorically with a meaningful percept. We applied neither global intensity normalization nor temporal high-pass filtering. The conditions were defined trial-by-trial on the basis of key presses performed by the subjects at the appearance and disappearance of a visual letter percept. We modeled five conditions per run (Figure 1): a prepercept (1) and a postpercept baseline (5), a prepercept hysteresis condition ([2], ranging from the contrast level at which subsequent drop out occurred to the contrast level at which pop out occurred), a supra-threshold condition ([3], between the contrast level for pop out and the same contrast level during contrast degradation), and a hysteresis condition ([4], ranging from the contrast level equivalent to that at which pop out occurred with increasing contrast to that at drop out during contrast degradation).

Percept-sensitive activity was defined by contrasting conditions 3 and 4 (percept present) against the three others (percept absent). This contrast $([3 + 4] - [1 + 2 + 5])$ corresponds to a simple boxcar function that starts with "OFF" (1 and 2) until the first pop out is reported, then switches to "ON" (3 and 4) and stays there until the drop out is reported when it reverts to "OFF" (5) until the next pop out, and so on and so forth. This means the data points are split into two populations as a function of whether the subject is perceiving a visual letter (3 and 4) or not (1, 2, and 5). Hysteresis in the perceptual time courses does not necessarily mean hysteresis in the fMRI signal of areas mapped this way. This is because the respective data points (from conditions 2 and 4) form a very minor fraction of the overall time course and are easily overridden by the rest of the data. Therefore, the occurrence of neural hysteresis was verified in the fMRI signal time courses from percept-sensitive areas (adjusted real-time course data) and in a dedicated contrast. This latter comparison contrasted hysteresis condition 4 against the prepercept hysteresis condition 2. The notion of hysteresis requires greater activity in this contrast and also perceptual responsiveness, which we verified by inclusive masking with the percept-sensitive activations (see above, at $p < 0.001$). Where appropriate, statistical inference was corrected for multiple nonindependent comparisons using Gaussian random field theory.

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