

Research Article

Temporally Unfolding Neural Representation of Pictorial Occlusion

Robert Rauschenberger,¹ Taosheng Liu,² Scott D. Slotnick,³ and Steven Yantis⁴

¹User Interface Design Center, Siemens Corporate Research, Princeton, New Jersey; ²Department of Psychology and Center for Neural Science, New York University; ³Department of Psychology, Boston College; and ⁴Department of Psychological and Brain Sciences, The Johns Hopkins University

ABSTRACT—*The human visual system possesses a remarkable ability to reconstruct the shape of an object that is partly occluded by an interposed surface. Behavioral results suggest that, under some circumstances, this perceptual process (termed amodal completion) progresses from an initial representation of local image features to a completed representation of a shape that may include features that are not explicitly present in the retinal image. Recent functional magnetic resonance imaging (fMRI) studies have shown that the completed surface is represented in early visual cortical areas. We used fMRI adaptation, combined with brief, masked exposures, to track the amodal completion process as it unfolds in early visual cortical regions. We report evidence for an evolution of the neural representation from the image-based feature representation to the completed representation. Our method offers the possibility of measuring changes in cortical activity using fMRI over a time scale of a few hundred milliseconds.*

Amodal completion is the perceptual mechanism by which a partly occluded shape is recovered. Most behavioral studies of amodal completion have used two-dimensional, or pictorial, occlusions (e.g., Guttman, Sekuler, & Kellman, 2003; Rauschenberger & Yantis, 2001; Sekuler & Palmer, 1992), which arise when one views depictions of occlusions. These studies suggest that the representation of a partly occluded surface proceeds from a representation of local image features corresponding to the visible part of that surface (including edges, local curvature, and T-junctions), and that this representation is

subsequently transmuted into a completed representation corresponding to the entire (reconstructed) contour and surface of the occluded object. For pictorial occlusions, this evolution has been found to occur over 200 to 400 ms. This relatively slow time course stands in contrast to the much more rapid course of amodal completion in three-dimensional scenes (Bruno, Bertamini, & Domini, 1997). The difference in processing speed can be explained by the fact that pictorial occlusions contain conflicting cues: Local features such as T-junctions suggest partial occlusion, whereas other sources of depth information favor a two-dimensional interpretation.

These behavioral results suggest that the corresponding neural representation of pictorial occlusion should evolve from one comprising local image features to one comprising a completed shape. The neural representation of amodally completed surfaces has been studied using both single-cell recordings and functional magnetic resonance imaging (fMRI). Both methods have provided evidence for the representation of the amodally completed object in early visual cortex (Bakin, Nakayama, & Gilbert, 2000; Kourtzi & Kanwisher, 2001; Lee & Nguyen, 2001; Sugita, 1999). However, to date, the evolution in time from a feature-based to a completed representation remains to be documented, and a recent report suggests that amodal completion at the neural level occurs very rapidly following stimulus onset (Lerner, Harel, & Malach, 2004).

We used an fMRI adaptation paradigm (Buckner et al., 1998), combined with brief, masked displays, to track the evolution of amodal completion. The logic of the fMRI adaptation paradigm is based on the finding that the sequential presentation of two stimuli that are functionally equivalent evokes a hemodynamic response (HDR) that is attenuated compared with that evoked by two stimuli that are not functionally equivalent. In this context, functional equivalence does not mean that the two stimuli in question are physically identical or even perceptually indis-

Address correspondence to Robert Rauschenberger, User Interface Design Center, Siemens Corporate Research, 755 College Rd. East, Princeton, NJ 08540, e-mail: robert.rauschenberger@siemens.com.

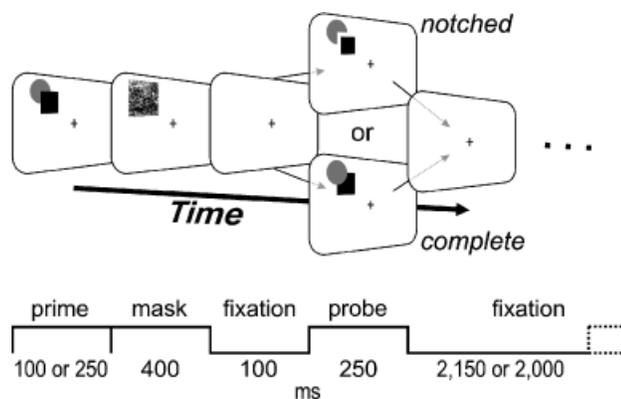


Fig. 1. Stimuli and procedure for the notched and complete conditions.

tinguishable, but rather that they receive equivalent internal representations (Kourtzi & Kanwisher, 2001).

We determined, at two different points in time (100 and 250 ms after stimulus onset), whether a partly occluded object is represented as a collection of local features explicitly present in the retinal image or as a completed shape in which occluded contours have been recovered. We accomplished this by observing the magnitude of HDR attenuation when a pictorial-occlusion prime was followed either by a stimulus whose local features unambiguously matched those of the prime or by a stimulus that unambiguously matched a completed interpretation of the prime. Accordingly, a pictorial-occlusion prime (notched disk abutting a square) was exposed for either 100 or 250 ms and was then followed by one of two unambiguous probe displays (see Fig. 1): either one corresponding to the completed interpretation of the preceding disk (*complete* condition: complete disk overlapping a square) or one corresponding to an unambiguously notched disk (*notched* condition: notched disk near a square). We refer to these conditions with a letter indicating the form of the probe (C for complete, N for notched) and the duration of the prime (100 or 250 ms).

If there were no evolution of the neural representation of the pictorial-occlusion prime, and the prime were treated as functionally equivalent to a complete disk even in brief exposures, the HDR evoked in the C100 condition would be comparable to that in the C250 condition (see Fig. 2a). In other words, there would be no difference in response to the complete-disk probe across exposure durations. Furthermore, if the prime's neural representation were complete almost immediately—even at 100-ms exposures—as has been claimed recently (Lerner et al., 2004), the response evoked in the C100 condition would be attenuated compared with that in the N100 condition (because the respective representations of the prime and probe stimuli are more similar to one another in the former condition than in the latter; Fig. 2a).

If, however, the neural representation of pictorial occlusion evolves over time, as suggested by behavioral data, a different

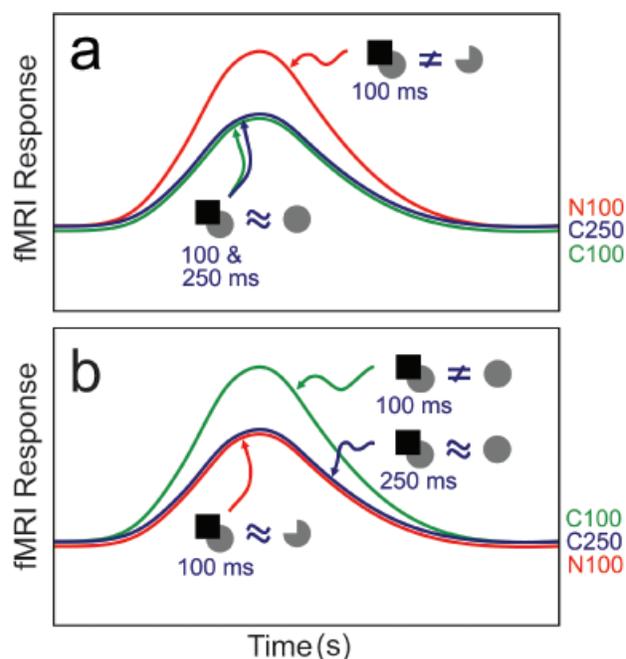


Fig. 2. Predicted functional magnetic resonance imaging (fMRI) response (a) if there is no evolution of the representation of pictorial occlusions and completion is nearly instantaneous and (b) if the processing of pictorial occlusions progresses from an initial representation of local image features to a completed representation of a shape that may include features that are not explicitly present in the retinal image. Predictions are shown only for the three critical conditions: notched probe after 100-ms prime (N100), complete probe after 100-ms prime (C100), and complete probe after 250-ms prime (C250). (See the main text for details.)

pattern of results should emerge. In this case, the HDR evoked in the C250 condition should be attenuated relative to that in the C100 condition, because the prime and probe representations are more similar to one another in the former condition, owing to amodal completion (see Fig. 2b). Similarly, the response in the N100 condition should also be attenuated relative to that in the C100 condition (which is the opposite of what would be predicted if no evolution occurs; cf. Figs. 2a and 2b)—again because there is a correspondence of the prime and probe representations in the former but not in the latter condition. In other words, a difference should be observed across exposure durations for the complete-disk probe, as well as between probe types at the brief exposure.

Consequently, the pattern of results across the C100, C250, and N100 conditions allows us to infer whether the representation of the pictorial-occlusion prime undergoes an evolution from a representation of local image features to a representation of an amodally completed shape. The inferences from the fourth condition (N250) are less straightforward, because the fate of the early representation remains controversial. According to one theory, the completed representation, once available, replaces the earlier representation (Sekuler & Palmer, 1992). In this case, the pictorial-occlusion prime would be represented as

equivalent to a notched probe only in short exposures, and the HDR in the N100 condition would be attenuated relative to the HDR in the N250 condition. According to an alternative *ambiguity* account, the pictorial-occlusion prime continues to be represented as notched at long exposures (in addition to being represented as completed), owing to the cue conflict entailed by pictorial occlusion (Gerbino, 1989). In this case, the pictorial-occlusion prime would be treated as equivalent to both the complete-disk and the notched-disk probes, and the HDR in the two conditions would be comparable. We return to this point in the Discussion.

METHOD

Imaging was performed on a 1.5-T Philips MRI scanner. For each subject, a high-resolution anatomic volume was obtained with a magnetization-prepared rapid gradient echo (MPRAGE) sequence (12.4-min acquisition; birdcage head coil; TR = 8.1 ms; TE = 3.7 ms; flip angle = 8°; 256-mm × 256-mm field of view; 256 × 256 acquisition matrix; 200 slices, 1 mm thick with no gap, yielding 1-mm isotropic resolution). Functional imaging was performed using an echoplanar imaging sequence (surface coil centered over occipital scalp; TR = 2 s; TE = 40 ms; flip angle = 90°; foot-to-head phase encoding; 192-mm × 192-mm field of view; 64 × 64 acquisition matrix; 33 slices, 3 mm thick with no gap, yielding 3-mm isotropic resolution). Following motion correction, slice-time correction, and functional-to-anatomic co-registration, the functional images and anatomic volume were transformed into Talairach space (Talairach & Tournoux, 1988). The anatomic volume was then segmented and reconstructed at the gray-matter/white-matter boundary, and subsequently flattened to yield a surface representation of the cortex (Kriegeskorte & Goebel, 2001). All analyses were performed using BrainVoyager (Maastricht, The Netherlands) on this flattened cortical representation.

Each of 10 subjects performed two different types of functional-localizer runs, one retinotopic-mapping run, and six event-related (Burock, Buckner, Woldorff, Rosen, & Dale, 1998) experimental runs (three runs each in the upper left and upper right quadrants, respectively). In all runs, subjects were instructed to maintain fixation on a central fixation cross. In the first of the two localizer runs, two disks were flashed on one 45° axis in opposite hemifields (duration: 200 ms, stimulus onset asynchrony: 800 ms) for 16 s; these alternated with two disks on the other 45° axis. The disks were of the same color, size, and eccentricity as those in the experimental runs (see the next paragraph). The two disks in the upper visual field were also in the same locations as the disks in the experimental runs and were used to localize the regions of interest (ROIs) in early visual cortex; the two disks in the lower visual field were used to balance the appearance of the stimulus. Cortical activity was localized using multiple regression by contrasting the regressor weights associated with each of the two stimulus configurations. Because the experimental stimuli were

restricted to the upper visual field, assessment of activity in early visual areas was restricted to the ventral occipital cortex. The second localizer run was modeled after previous studies (Kourtzi & Kanwisher, 2001) in which the lateral occipital complex (LOC) was localized using a general linear model analysis with a contrast between regressors associated with intact versus fragmented shapes; the stimuli were taken from Kourtzi and Kanwisher (2001). The statistical threshold was set to $p < .001$ (uncorrected) for contrasts in both localizers. Borders between visual areas were obtained using an independent retinotopic-mapping scan, using the bifield stimulation technique (Slotnick & Yantis, 2003).

During the experimental runs, a pictorial-occlusion prime (a square abutting a notched disk) was presented for either 100 or 250 ms, followed by a 400-ms noise mask, and then a 100-ms fixation display. The probe (250 ms in duration) was either a complete disk overlapping a square or a notched disk standing separate from the square (Fig. 1). Both the diameter of the disk and one side of the square subtended 1.2° of visual angle. Squares were red and disks green, presented on a black background. The probe and prime were both presented in the upper left or upper right quadrant, with the center of the disk 2° from fixation. There were four different stimulus orientations (disk at top left, top right, bottom left, or bottom right of square), thus providing variability in the stimulus. A trailing fixation display was presented for either 2,150 or 2,000 ms, depending on the exposure duration of the prime (constraining the duration of each trial to be 3,000 ms).

Null trials were included in addition to the four experimental conditions to create between-trial temporal jitter (Kourtzi & Kanwisher, 2001). The five trial types were pseudorandomly intermixed such that each trial type was preceded and followed equally often by every other trial type. Approximately 48 trials were presented for each condition in each quadrant. The subject's task, designed to enhance attention to the stimuli, was to indicate whether the second stimulus (the probe) contained a complete or notched disk, by pressing one of two buttons of a response pad.

For each subject, event-related time courses (expressed as percentage signal change) for each experimental condition were calculated in independently defined ROIs, using the activity at event onset (time 0) as baseline (Slotnick & Schacter, 2004). Event-related activity was interpolated, yielding 1-s temporal resolution. ROIs in the left and right hemispheres were used to obtain event-related averages corresponding to stimuli in the right and left hemifields, respectively. There was no qualitative difference in data from the two hemispheres; therefore, we collapsed data from the two hemispheres of each subject and computed group mean time courses.

RESULTS

Early visual areas (V1, V2, VP, V4v, and LOC) were localized separately for each subject and served as ROIs for the analysis of

HDR attenuation. As seen in Figure 3a, there was a clear qualitative divide between the event-related activity associated with the C100 condition and the activity associated with the remaining conditions, which all exhibited marked attenuation relative to the C100 condition. The somewhat more gradual return to baseline for the nonattenuated (or less attenuated) condition (C100) is a relatively common finding (e.g., Kourtzi & Kanwisher, 2001) that is to be expected because of the larger deviation from baseline in this condition than in the conditions evidencing attenuation. In brief, these results indicate that the neural representation of the pictorial-occlusion prime changed with time, from one corresponding to a notched disk to one corresponding to a complete disk (cf. Figs. 3a and 2b).

To assess the statistical significance of these effects, we limited analysis a priori to the mean level of activity 5 s following event onset (Kourtzi & Kanwisher, 2001). (The same pattern of results was obtained using the mean activity 4–6 s following event onset.) The mean event-related activity at the 5-s time point within each ROI is shown in Figure 3b. A two-way analysis of variance (ANOVA) with visual area and condition as factors

revealed significant main effects of visual area, $F(4, 28) = 3.53$, $p < .025$, $\eta^2 = .34$, and condition, $F(3, 21) = 9.84$, $p < .0005$, $\eta^2 = .58$, but no significant interaction ($F < 1$).

The main effect of condition reflects the larger event-related activity in the C100 condition compared with the other three conditions: V1— $F(1, 8) = 12.09$, $p < .01$, $\eta^2 = .60$; V2— $F(1, 8) = 28.59$, $p < .001$, $\eta^2 = .78$; VP— $F(1, 8) = 17.08$, $p < .005$, $\eta^2 = .69$; V4v— $F(1, 7) = 9.55$, $p < .025$, $\eta^2 = .58$; LOC— $F(1, 9) = 8.55$, $p < .025$, $\eta^2 = .49$. (Note that not all observers exhibited localizer activity in all ROIs. Some of the comparisons were therefore limited to a subset of the observers.) At the same time, none of the other three conditions differed significantly from one another: V1— $F < 1$; V2— $F(2, 16) = 2.18$, n.s.; VP— $F < 1$; V4v— $F < 1$; LOC— $F < 1$. These effects were consistent across visual areas, as illustrated by the lack of a significant interaction between visual area and condition (see the previous paragraph). Notably, they were found even at the earliest levels in the cortical visual hierarchy (V1 and V2).

The main effect of visual area in the two-way ANOVA is attributable to the overall smaller event-related response in LOC

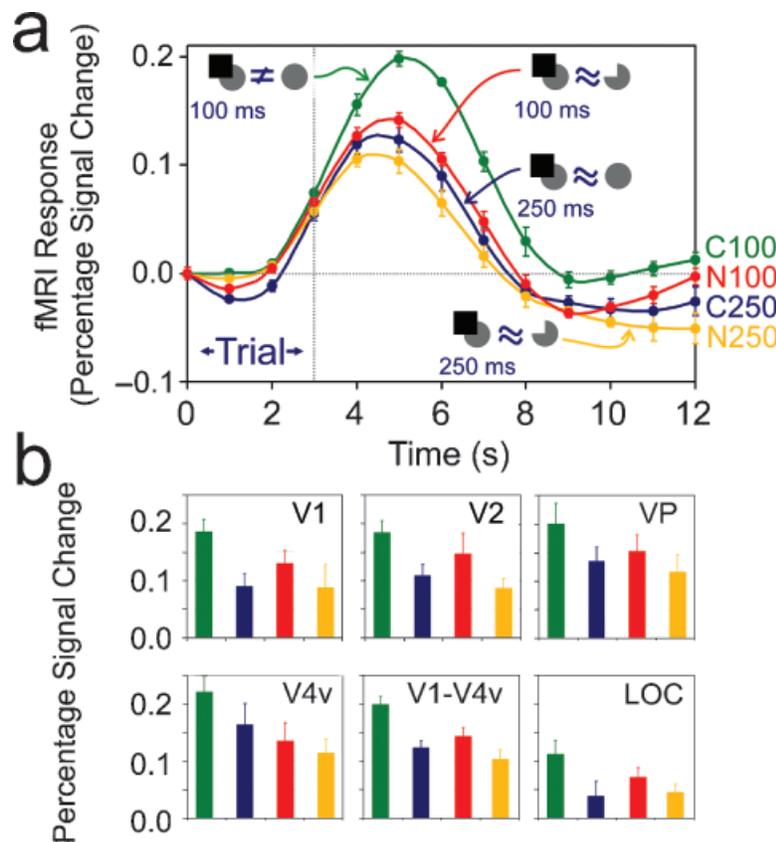


Fig. 3. Event-related functional magnetic resonance imaging (fMRI) response in regions of interest (ROIs): (a) time courses associated with the four trial types (N100— notched probe after 100-ms prime, N250— notched probe after 250-ms prime, C100— complete probe after 100-ms prime, and C250— complete probe after 250-ms prime), averaged across retinotopic visual areas (V1, V2, VP, V4v) and subjects, and (b) mean event-related activity 5 s after event onset, estimated separately for each ROI, including lateral occipital cortex (LOC). The bottom central panel (V1–V4v) corresponds to the functions shown in (a). Error bars show standard errors.

compared with the early retinotopic areas (V1, V2, VP, and V4v; Fig. 3b). Accordingly, an identical ANOVA excluding LOC revealed no significant effect of visual area ($F < 1$), while retaining the significant main effect of condition, $F(3, 21) = 11.16, p < .0005, \eta^2 = .61$, and the nonsignificant interaction between visual area and condition ($F < 1$). Because the interaction continued to be nonsignificant, we collapsed across visual areas for all further comparisons reported in the next section.

DISCUSSION

The results show that the neural representation of pictorial occlusion evolves over time. At the brief exposure, a notched-disk probe elicited an attenuated response relative to a complete-disk probe (N100 < C100), $F(1, 8) = 25.39, p < .001, \eta^2 = .76$, indicating that the pictorial-occlusion prime was represented as notched in brief exposures. A complete-disc probe elicited an attenuated response at the long exposure relative to the brief exposure (C250 < C100), $F(1, 8) = 26.29, p < .001, \eta^2 = .77$, indicating that the pictorial-occlusion prime was represented as completed in long exposures (cf. Fig. 2b). (The relatively small HDR in the C250 condition rules out the possibility that the similarly small response for the notched-disk probe was due to its relatively smaller area or related factors.) Note that the very same stimulus pair (pictorial occlusion-complete disk) produced strikingly different results depending on the exposure duration, as would be expected if the representation of the prime evolved over time.

Because we used the pattern of results across a number of conditions to infer the representation of the pictorial-occlusion prime at different points in time, our study has no absolute baseline against which all the experimental conditions can be compared. It is possible, therefore, that the HDR in the C100 condition, which evoked the highest level of activity among all conditions, was itself attenuated relative to a completely-different baseline. This would be the case if, on a proportion of trials, the pictorial-occlusion prime were represented as completed even in brief displays (cf. Rauschenberger, Peterson, Mosca, & Bruno, 2004).

Our conclusions are based on the assumption that the responses evoked in the C250, N100, and N250 conditions were attenuated relative to an absolute baseline or, at least, to the response in the C100 condition. Might it be the case, however, that the response in the C100 condition was elevated relative to the remaining conditions? The only plausible explanation for such an elevation is an attentional enhancement of the HDR in the C100 condition relative to the other conditions. However, it is quite unlikely that attention is responsible for the observed pattern of results. The stimuli in our study were identical within pairs of conditions, and the stimuli in the C100 condition were the same as those in the C250 condition. Thus, one would have to propose that short exposures are inherently more attention demanding than long exposures; however, one would then have to

explain why the response in the N100 condition was not also elevated. Hence, to explain the observed pattern of results as due to an elevated response in the C100 condition, one must argue that a complete disk is inherently more attention demanding than a notched disk is, but only when it is preceded by a brief exposure of another stimulus. We see no a priori grounds for making such an assumption, whereas the patterns we observed can be accounted for by an evolving representation of the prime stimulus over time.

As mentioned earlier, interpreting the results of the N250 condition is not as straightforward as interpreting the results of the other three conditions. Statistical analysis revealed that the HDR was significantly attenuated in this condition relative to the C100 condition, $F(1, 8) = 47.36, p < .0005, \eta^2 = .86$. Indeed, the fMRI response in this condition strongly resembled that in the N100 condition, $F(1, 8) = 4.03, n.s.$ These results suggest that the occluded prime supported adaptation of the notched probe even at the long exposure. This conclusion is consistent with several recent behavioral studies suggesting that both an image-based (2-D) representation and an amodally completed (3-D) representation of the stimulus arise at long exposure durations (Gerbino, 1989; Rauschenberger et al., 2004). Some caution, however, must be exercised in interpreting the results of the N250 condition. It is not known how long fMRI adaptation effects last; because fMRI adaptation was present at 100 ms, it might still have been present in the 250-ms exposure.

If the early visual cortical areas indeed sustain both representations concurrently, it is conceivable that higher areas sustain only the representation that is consciously perceived at any given moment. Single-cell studies of perceptual ambiguity have shown that early visual neurons respond to both interpretations of an ambiguous stimulus, whereas the response of higher visual neurons is tied to the representation currently dominating in conscious perception (Sheinberg & Logothetis, 1997). Our selection of relatively early visual areas as ROIs (V1 to LOC), however, does not permit us to determine whether this is also the case for pictorial-occlusion stimuli, which are, in some sense, perceptually ambiguous (Rauschenberger et al., 2004). Therefore, if a single (completed) representation exists in higher visual areas, we suggest that it might be found in regions located more anterior to LOC within the ventral visual processing stream.

A recent study by Lerner et al. (2004) investigated the time course of perceptual completion using fMRI but failed to find evidence of a protracted evolution of the neural representation of pictorial occlusion. In that study, the HDR to intact, scrambled, and “partially occluded” stimuli, respectively, was measured. The scrambled displays contained thick occluding stripes that were identical to those used in the partially occluded condition. The only difference between these two types of displays was that the image segments in the partially occluded condition possessed good continuity between the image fragments, so that these could potentially be completed into a meaningful whole,

whereas the image segments in the scrambled displays were disparate fragments that did not afford completion into any meaningful whole. Lerner et al. found that the HDR in LOC was greater for partially occluded stimuli than for scrambled stimuli. Moreover, this relationship did not change with exposure duration (60 vs. 250 ms, masked), and the authors deduced that the extent of “completion” was similar for the long and short durations.

A possible explanation for the discrepancy between this conclusion and that of the present study, as well as previous behavioral work on amodal completion (e.g., Sekuler & Palmer, 1992), is that the results of Lerner et al. (2004) might have reflected object recognition rather than amodal completion. It is known that the HDR in area LOC varies with the recognizability of a stimulus (Grill-Spector, Kushnir, Hendler, & Malach, 2000). Indeed, this was the rationale for the experiment of Lerner and her colleagues. It is also known that the deletion of components of an object does not (necessarily) impair object recognition if the proper spatial relationship between the remaining components is maintained (Biederman, 1987). For example, the recognizability of the partially occluded stimuli might not have been much different if the occluding strips had been replaced by blank regions. Hence, even without needing to invoke amodal completion, one might predict that recognition of the partially occluded stimuli would be superior to that of the scrambled stimuli and that, concomitantly, the HDR would be greater for the former than the latter. Consistent with this prediction, subjects' recognition performance for each stimulus condition mapped largely onto the HDR in that condition.

Our finding that the completed representation is expressed (after 250 ms) as early as V1 accords well with the single-cell literature (Bakin et al., 2000; Lee & Nguyen, 2001; Sugita, 1999). At the same time, it appears to stand in contrast to results of other fMRI studies (e.g., Mendola, Dale, Fischl, Liu, & Tootell, 1999) that have revealed little preferential activation in V1 and V2 in response to illusory contours, a phenomenon widely viewed as related to amodal completion. More recent studies, however, have called these null findings into question (Pillow & Rubin, 2002; Stanley & Rubin, 2003) and there have been fMRI reports of activation to illusory contours in V1 and V2 (Hirsch et al., 1995; Seghier et al., 2000). The present results corroborate evidence that early visual areas are indeed involved in the processing of amodal completion, whether via feedback connections (Lee & Nguyen, 2001) or intraregional processing in V1 and V2 (Stanley & Rubin, 2003).

Our findings of fMRI adaptation in V1 might seem somewhat surprising in light of a recent failure to elicit fMRI adaptation in V1 (Boynton & Finney, 2003). However, the authors of that study, which tested for orientation-specific adaptation, pointed out that the lack of adaptation effects in V1 could have been due to an insensitivity of V1 cells, but not the cells in later areas, to the orientations and spatial frequencies used (Boynton & Finney, 2003, p. 8785). Hence, whether fMRI adaptation can be

observed in V1 may depend at least in part on the stimuli that are used to evoke it. Furthermore, in contrast to Boynton and Finney, we did not test for orientation-specific adaptation effects. Also, unlike the simple grating stimuli used in their study, our pictorial-occlusion stimuli can potentially lead to top-down feedback or interregional processing, which might facilitate adaptation effects in V1.

Finally, our results show that it is possible to examine neural processes at a very rapid time scale using fMRI, which is typically thought to have an effective temporal resolution of no fewer than 1 to 2 s because of the sluggish HDR. In our study, the combination of brief masked exposures and an adaptation paradigm tracked neural representations separated by as little as 150 ms. The key to investigating the unfolding of neural events on a small time scale using fMRI may therefore lie in taking “snapshots” of the evolving representation—in a sort of freeze-action sequence—rather than tracing the time course of these events in real time using the HDR function directly. This approach may prove a fruitful avenue toward increasing the temporal resolution of fMRI.

Acknowledgments—This work was supported by National Institutes of Health Grant R01-DA13165 to S.Y. and National Science Foundation Grant 0418179 to R.R. We thank Z. Kourtzi and N. Kanwisher for providing their LOC-localizer stimuli, and J. Serences for the retinotopic-mapping program.

REFERENCES

- Bakin, J.S., Nakayama, K., & Gilbert, C.D. (2000). Visual responses in monkey areas V1 and V2 to three-dimensional surface configurations. *Journal of Neuroscience*, *20*, 8188–8198.
- Biederman, I. (1987). Recognition-by-components: A theory of human image understanding. *Psychological Review*, *94*, 115–147.
- Boynton, G.M., & Finney, E.M. (2003). Orientation-specific adaptation in human visual cortex. *Journal of Neuroscience*, *23*, 8781–8787.
- Bruno, N., Bertamini, M., & Domini, F. (1997). Amodal completion of partly occluded surfaces: Is there a mosaic stage? *Journal of Experimental Psychology: Human Perception and Performance*, *23*, 1412–1426.
- Buckner, R.L., Goodman, J., Burock, M., Rotte, M., Koutstaal, W., Schacter, D., Rosen, B., & Dale, A.M. (1998). Functional-anatomic correlates of object priming in humans revealed by rapid presentation event-related fMRI. *Neuron*, *20*, 285–296.
- Burock, M.A., Buckner, R.L., Woldorff, M.G., Rosen, B.R., & Dale, A.M. (1998). Randomized event-related experimental designs allow for extremely rapid presentation rates using functional MRI. *NeuroReport*, *9*, 3735–3739.
- Gerbino, W. (1989). Form categorization and amodal completion. *Acta Psychologica*, *72*, 295–300.
- Grill-Spector, K., Kushnir, T., Hendler, T., & Malach, R. (2000). The dynamics of object-selective activation correlate with recognition performance in humans. *Nature Neuroscience*, *3*, 837–843.
- Guttman, S.E., Sekuler, A.B., & Kellman, P.J. (2003). Temporal variations in visual completion: A reflection of spatial limits? *Journal of Experimental Psychology: Human Perception and Performance*, *29*, 1211–1227.

- Hirsch, J., DeLaPaz, R.L., Relkin, N.R., Victor, J., Kim, K., Li, T., Borden, P., Rubin, N., & Shapley, R. (1995). Illusory contours activate specific regions in human visual cortex: Evidence from functional magnetic resonance imaging. *Proceedings of the National Academy of Sciences, USA*, *92*, 6469–6473.
- Kourtzi, Z., & Kanwisher, N. (2001). Representation of perceived object shape by the human lateral occipital complex. *Science*, *293*, 1506–1509.
- Kriegeskorte, N., & Goebel, R. (2001). An efficient algorithm for topologically correct segmentation of the cortical sheet in anatomical MR volumes. *NeuroImage*, *14*, 329–346.
- Lee, T.S., & Nguyen, M. (2001). Dynamics of subjective contour formation in the early visual cortex. *Proceedings of the National Academy of Sciences, USA*, *98*, 1907–1911.
- Lerner, Y., Harel, M., & Malach, R. (2004). Rapid completion effects in human high-order visual areas. *NeuroImage*, *21*, 516–526.
- Mendola, J.D., Dale, A.M., Fischl, B., Liu, A.K., & Tootell, R.B. (1999). The representation of illusory and real contours in human cortical visual areas revealed by functional magnetic resonance imaging. *Journal of Neuroscience*, *19*, 8560–8572.
- Pillow, J., & Rubin, N. (2002). Perceptual completion across the vertical meridian and the role of early visual cortex. *Neuron*, *33*, 805–813.
- Rauschenberger, R., Peterson, M.A., Mosca, F., & Bruno, N. (2004). Amodal completion in visual search: Preemption or context effects? *Psychological Science*, *15*, 351–355.
- Rauschenberger, R., & Yantis, S. (2001). Masking unveils pre-amodal completion representation in visual search. *Nature*, *410*, 369–372.
- Seghier, M., Dojat, M., Delon-Martin, C., Rubin, C., Warnking, J., Segebarth, C., & Bullier, J. (2000). Moving illusory contours activate primary visual cortex: An fMRI study. *Cerebral Cortex*, *10*, 663–670.
- Sekuler, A.B., & Palmer, S.E. (1992). Perception of partly occluded objects: A microgenetic analysis. *Journal of Experimental Psychology: General*, *121*, 95–111.
- Sheinberg, D.L., & Logothetis, N.K. (1997). The role of temporal cortical areas in perceptual organization. *Proceedings of the National Academy of Sciences, USA*, *94*, 3408–3413.
- Slotnick, S.D., & Schacter, D.L. (2004). A sensory signature that distinguishes true from false memories. *Nature Neuroscience*, *7*, 664–672.
- Slotnick, S.D., & Yantis, S. (2003). Efficient acquisition of human retinotopic maps. *Human Brain Mapping*, *18*, 22–29.
- Stanley, D.A., & Rubin, N. (2003). fMRI activation in response to illusory contours and salient regions in the human lateral occipital cortex. *Neuron*, *23*, 323–331.
- Sugita, Y. (1999). Grouping of image fragments in primary visual cortex. *Nature*, *401*, 269–272.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme.

(RECEIVED 2/10/05; REVISION ACCEPTED 5/11/05;
FINAL MATERIALS RECEIVED 6/1/05)