The "Mosaic Stage" in Amodal Completion as Characterized by Magnetoencephalography Responses

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Abstract

■ We investigated the process of amodal completion in a same–different experiment in which test pairs were preceded by sequences of two figures. The first of these could be congruent to a global or local completion of an occluded part in the second figure, or a mosaic interpretation of it. We recorded and analyzed the magnetoencephalogram for the second figures. Compared to control conditions, in which unrelated primes were shown, occlusion and mosaic primes reduced the peak latency and amplitude of neural activity evoked by the occlusion patterns. Compared to occlusion primes, mosaic ones reduced the latency but increased the amplitude of evoked neural activity. Processes relating to a mosaic interpretation of the occlusion pattern, therefore, can dominate in an early stage of visual processing. The results did not provide evidence for the presence of a functional "mosaic stage" in completion per se, but characterize the mosaic interpretation as a qualitatively special one that can rapidly emerge in visual processing when context favors it. ■

INTRODUCTION

The human brain has the capacity to fill in what the eye cannot see. A visual object appears whole and complete even when its contour is partly occluded by another shape. This type of completion is called amodal completion because the occluded part seems present, although the perceiver has no visual sensation of it (Michotte, Thines, & Crabbe, 1964; Michotte & Burke, 1951). Amodal completion does not happen instantaneously; the process extends long enough to be measurable in psychophysiological and behavioral studies (Murray, Sekuler, & Bennett, 2001; Sekuler & Palmer, 1992). The estimated durations range from more than 200 msec in priming studies using simple pictorial displays (Sekuler & Palmer, 1992) to less than 100 msec for occlusion patterns viewed binocularly with a disparity between the two retinal inputs that suggested different depths for occluded and occluding figure (Bruno, Bertamini, & Domini, 1997) and 75 msec in a psychophysical task in which participants judged whether a partly occluded square was higher than its width (Murray, Sekuler, & Bennett, 2001).

A debate has evolved over whether separate stages can be distinguished in the completion process. Sekuler and Palmer (1992) suggested that completion is preceded by a mosaic stage, in which the figure is represented as a two-dimensional shape. In a primed-matching paradigm these authors found that when an occluded figure is briefly presented (<100 msec) and followed by a same–different task, the effect of the prime on response time (RT) was similar to that of a mosaic figure. Crucially, this was not the case for longer presentation times of the occluded figure (>200 msec). For longer presentations, the perceptual system may have developed an amodal representation of a whole figure behind the occluder, facilitating responses to whole figures in the test pair, but not mosaic ones.

Additional support for a mosaic stage has come from visual search studies. Whereas brief, masked, presentation of a search display allows the detection of mosaic shapes contained in partly occluded figures (Rauschenberger & Yantis, 2001), prolonged presentation typically preempts their detection (Rensink & Enns, 1998; He & Nakayama, 1992). This result suggests that the mosaic representation precedes completion and is inaccessible once completion has finished.

The existence of a serial "mosaic stage" is under debate, however, because the shortest estimates seem to leave little time for functionally discrete stages. Recent neuroimaging studies seem to favor the short estimates; a functional magnetic resonance imaging (fMRI) study showed effects of amodal completion in higher order visual areas using masks and presentation latencies as short as 60 msec (Lerner, Harel, & Malach, 2004). These times seem too fast for the process to contain a discrete, serial mosaic stage. On the other hand, fMRI data are inconclusive, as they lack the appropriate temporal resolution.

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At least some findings that initially suggested a mosaic stage may in fact have resulted from context effects. In a more recent study (Rauschenberger, Peterson, Mosca, & Bruno, 2004), the authors recast their original interpretation of the finding that masking makes mosaic interpretations accessible (Rauschenberger & Yantis, 2001). Their new work provides evidence that surrounding figures in search displays can bias the target figure to one or another interpretation. What was initially understood as evidence for a distinct early stage in the completion process may therefore have been an effect of surrounding context on the completion process, biasing it toward one of the alternative interpretations computed in parallel.

Given these results, what is the status of the mosaic stage? In our view, the new and the old interpretation of the (Rauschenberger & Yantis, 2001) data are not necessarily mutually exclusive. It is possible, for instance, that alternative interpretations, including a mosaic interpretation, are processed in parallel, and yet the latter may be computed at a faster rate than the others, such that it is dominant in neural activity until the completion interpretations become available. Depending on whether the task taps activity before or after the completion interpretations are available, behavioral responses could then show (or fail to show) the effects of contextual bias. This still leaves open, in principle, the possibility of early mosaic interpretations that are inhibited by contextual bias in a later stage.

In addition to spatial context (Rauschenberger, Peterson, et al., 2004), it is known that temporal context can affect the interpretation of an occluded figure (Zemel, Behrmann, & Mozer, 2002; Joseph & Nakayama, 1999). We previously investigated whether these effects work on visual processes, that is, that they are not late, top-down processes. To that extent we presented two figures, an unoccluded followed by an occluded one, prior to a test pair in a primed-matching paradigm (Plomp & van Leeuwen, in press). The first of the two figures preceding the test pair could be an occlusion or mosaic interpretation of the following occluded figure. When this was the case, the two figures had a combined priming effect on RT to the same–different task that was larger than their individual ones. This overadditive character of the priming effect was taken as evidence that the first figure directly influences the processing of the following, occluded figure.

In the typical primed-matching task (Beller, 1971), the priming effects are solely on the test pair. Our study differs from this in that two figures precede the test pair, allowing for priming effects of the first on the second figure, although these are not targets of the matching task. By keeping the priming effects on the second figure separate from the task, we can assure that facilitatory effects on this figure are not due to changes in response-related mechanisms.

In Plomp and van Leeuwen (in press), the priming effect on occluded figures occurred with occlusion as well as mosaic primes. This suggested that, besides completion, mosaic interpretations are also present in the system, possibly processed in parallel. Mosaic interpretations may dominate briefly over alternative completion interpretations if the former is achieved at a faster rate than the latter. To investigate this hypothesis, we need to consider neural events that take place in the processing of partly occluded figures, specifically, how their evoked responses are modulated by preceding figures congruent to one of their interpretations. For partly occluded moving gratings it has been shown that brain activity changes with different interpretations that are induced by small changes in the spatial context (Duncan, Albright, & Stoner, 2000). This study, although it was concerned with motion perception, provides evidence that contextual effects on amodal completion are reflected in brain activity. For static figures, however, the difference between priming one or the other interpretation may be quite subtle. Our focus on small changes in the processing of the same, static figure therefore calls for a measure of brain activity with high temporal as well as spatial resolution.

In the present study, we used magnetoencephalography (MEG) to record the evoked response of occluded figures under different priming conditions. Following the paradigm of Plomp and van Leeuwen (in press), we primed three interpretations of the figures: two completion interpretations and the mosaic one. We hypothesized that if an early, serial, mosaic stage can be primed then the evoked brain activity would decrease and come faster than when completion interpretations are primed. In addition, if a distinction between the effects of the two completion primes (global and local) is observed, this would suggest an even further differentiation within the completion process. In this way, differences between primed interpretations could help characterize the process of amodal completion in the brain and clarify the status of the mosaic stage.

METHODS

Participants

Ten male volunteers participated; all of them were right-handed, healthy individuals with normal or corrected-to-normal vision and no reported history of neurological deficits. Their ages ranged from 25 to 62 years with a median of 30 years. Informed consent was obtained from all participants before the experiment. The ethics committee of RIKEN approved of all procedures.

Stimuli and Design

The stimuli consisted of two occluded figures, a cross-shaped and a circle-shaped one, and for each of them three corresponding simple figures. Each corresponded to one possible interpretation of the occluded figure: as a global completion (based on an optimization of the amount of symmetry axes in the partly occluded figure), as a local completion (based on the good continuation of lines at the point of occlusion), or as a mosaic (a two-dimensional cutout figure). In the remaining text, we will refer to occluded figures using the more neutral term composite figures, as they can be given a mosaic interpretation as well.

The size of the occluded region is a determinant of completion time (Guttman, Sekuler, & Kellman, 2003; Shore & Enns, 1997). We therefore selected composite figures in which the amount of occlusion was not confounded with the local or global nature of the completion. The amount of occlusion was larger for the cross-shaped global completion (25%) than for the corresponding local one (15%), whereas this was reversed for the circle-shaped figure; the amount of occlusion in the local completion (32%) was larger than for the corresponding global completion (22%). The control figures were a square identical to the one in the composite figure and, alternatively, two small black patches. All stimuli used in the experiment are depicted in Figure 1.

The experiment was an extension of the primed matching paradigm (Beller, 1971) in which participants decided whether two simultaneously presented figures were same or different. Before this test pair, participants were briefly presented two figures, one after the other. We varied the congruency of these two figures to the test pair. In experimental conditions, a simple figure and a composite figure preceded the test pair and the former always corresponded to an interpretation (one of two possible completions or a mosaic interpretation) of the latter. In these conditions, both figures were congruent to the test pair, and therefore congruent to each other. Congruency of the simple to the composite figure was expected to change the processing of the composite and result in a subsequent decrease in RT to the test pair. In control conditions, the preceding figures were either two patches and a composite figure or a square and a composite figure. In these conditions, only the composite figure was congruent to the test pair. The patches primed for the occurrence of the composite figure without having overlap with its contours. The square appeared in the same location as the square in the subsequent composite, overlapping with approximately half of the contour of the composite figure while being neutral with respect to its alternative interpretations. This controlled for the possibility that overlapping contours can account for any priming effects of the simple figures on the evoked response of composite figures in the experimental condition. The control conditions thus controlled for the effect of congruency on RT as well as on the evoked response of the composite figure. In baseline conditions, two blank screens briefly replaced the fixation point; that is, no figures were presented before the test pair while the timeline of a trial was left intact. This condition served to assess the effect of congruent preceding figures on RTs.

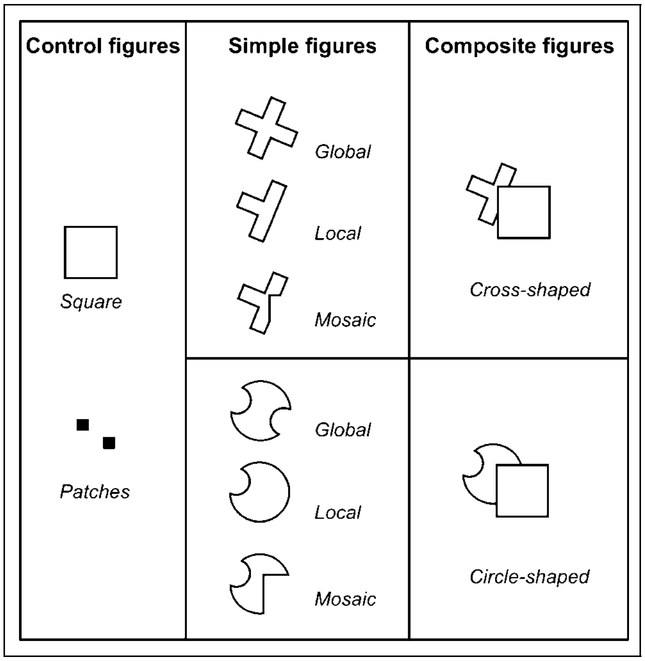

Figure 1. The stimuli. Top right, the cross-shaped composite figure and its three interpretations (simple figures); bottom right, the circle-shaped figures. Control figures are depicted on the left.

The experiment consisted of 22 runs of which 6 contained only baseline trials. The others contained both control and experimental trials. The baseline runs were presented at regular intervals between the other ones and the order of the runs differed for each participant.

In control/experimental runs each composite figure could be preceded by four different simple figures, those corresponding to its three interpretations and one of the two control figures. These figures were presented in a fixed orientation. Composite figures were always congruent to the test pair. For the simple figure, this was the case in three out of four trials; the control figure being incongruent and the three simple figures being congruent to the test pair. These characteristics encouraged attention to the preceding sequence of figures, although they were not explicitly part of the task.

Within a control/experimental run the two composite figures were paired with a different control stimulus. This pairing was fixed within runs, but changed between runs. Within runs, the contingency between the first and second figure was therefore the same in the control as in the experimental trials. The occurrence of control figures was counterbalanced across runs so that they appeared equally frequent as each simple figure in the total experiment. The eight unique trials in a run were repeated eight times and the resulting 64 trials lasted approximately 4 min.

Test pairs consisted of two simultaneously presented simple figures. "Different" pairs consisted of two simple figures from the same figure class. Each different pair was coupled to a "same" pair so that its contingency with the preceding figure was the same. All test pairs appeared equally often throughout the experiment.

Half of the test pairs within a run were same and half were different pairs. They appeared rotated counterclockwise with respect to the preceding figures. This way, low-level stimulus attributes varied between the displays, ensuring that any facilitation of RT was not based on low-level features. In our previous work (Plomp & van Leeuwen, in press) we showed that despite this difference in orientation it is possible to obtain priming effects for completion and mosaic interpretations of the composite alike (cf. Sekuler & Palmer, 1992, Experiment 3).

Apparatus

The experiment was conducted in a magnetically shielded room while the participant sat in a comfortable and supportive chair. On both armrests, an optical sensor was mounted to register responses. The stimuli were projected onto a 17-in. display with a refresh rate of 60 Hz using an XGA LCD projector and a mirror system. The precise timing of the presentation was controlled with a page-cycling routine of a Visual Stimulus Generator (Cambridge Software, Rochester, UK). A photodiode was attached to the screen to mark the exact stimulus onset times. The composite figures spanned 2.5° of visual angle; the figures in the test pair were presented 4.5° apart.

We recorded MEG signals using an Omega whole head 151-sensor system (CTF Systems Inc., Vancouver, BC, Canada). Additional electrodes monitored vertical eye movement (electrooculogram [EOG] electrodes 1 cm above and below the left eye), horizontal eye movement (EOG electrodes 1 cm lateral to the left and right outer canthus of the eyes), and heart function (ECG electrodes, left and right wrists, left ankle and lead V2). Before the experiment, three head coils were attached to the participant's scalp (at the nasion and both preauricular points) that served as a reference coordinate system. The MEG signal was low-passed at 200 Hz and digitized at 625 Hz. The resulting signal was recorded throughout the complete run and stored on a workstation.

Procedure

Before the recording, participants practiced the experiment inside the shielded room until they understood the procedure. A trial started with a 500-msec fixation point, followed by a 50-msec presentation of the first figure. A 300-msec interval separated the simple and the composite figure. This figure was presented for 50 msec, and after a 500-msec interstimulus interval the test pair appeared centered on the screen.

The composite figures were presented with the occluded part centered on the screen. The preceding figures in the experimental condition overlapped with that part. In the control condition, the position of the square figure was identical to that of the square in the composite figure; for the patches the lower one was located where the center of the square would appear.

Participants judged as quickly and as accurately as possible whether the two figures were the same or different. Half of the participants responded "same" by lifting their right index finger, the other half with the left. After 1 sec, the right answer appeared on the screen, lasting for 400 msec. A trial then concluded with a 200-msec blank screen after which the following trial began. An example of a trial is depicted in Figure 2. Every 16 trials, a smiling icon appeared on the screen for 4 sec to provide rest to the eyes and break the chain of presentations. The order of the trials within a run was randomized and different for each participant.

MEG Signal Analysis

Signal Processing

Environmental noise was first removed from the MEG signal by forming the third gradient of the magnetic field and then the resulting data were filtered in the 1- to 200-Hz band using the CTF software. Notch filters were

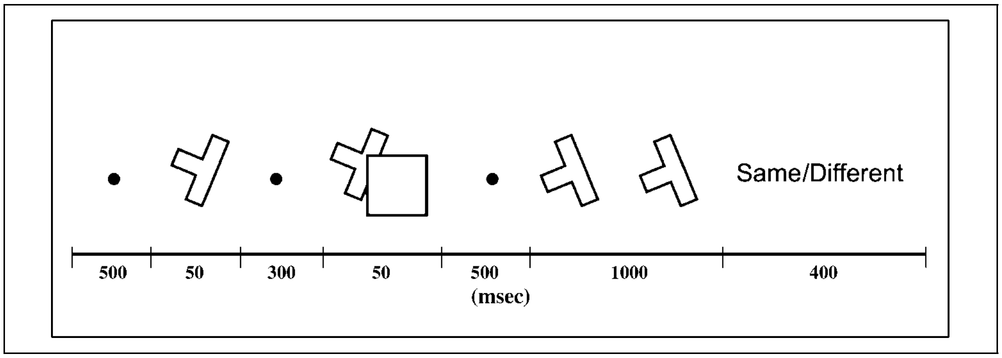

Figure 2. Example of an experimental trial where the test pair is preceded by a composite figure and a figure congruent to its local interpretation.

applied at 50 and 90 Hz and their harmonics to remove noise from the power line and the data projector. Noisy sensors were identified and excluded from further analyses. The continuous recordings of a run were divided into trials covering an interval from 100 msec before onset of the first stimulus to 300 msec after test pair onset. Trials containing blinks or eye movements during this period were excluded from further analysis. Artifacts generated by background physiological activity (e.g., heartbeat) were removed using independent component analysis (Jahn, Cichocki, Ioannides, & Amari, 1999). Within runs, the trials of the same condition were averaged, resulting, across runs, in 10 types of averaged signals (three experimental plus two control conditions for each of the two composite figures). There were eight trials for each condition in a run but if more than three of those were removed due to eye movements then the average of this particular condition was not analyzed further.

Signal-to-Noise Ratio–Based Selection

For further analyses, we selected sensors based on their signal-to-noise ratio (SNR). The SNR was defined as the mean amplitude divided by its standard deviation in a 20-msec window. The center of the window was moved in 1.6-msec steps through the 50- to 300-msec interval after the onset of the composite figure. If a sensor had a high SNR peak value this sensor was considered to have higher signal content compared to background noise, and thus to be more responsive to the presented stimulus. We extracted the MEG signal for the 10 sensors with the highest SNR for every condition within each run of every participant. This resulted in a list of most responsive sensors. The analysis concerned the peak amplitudes and latencies of the 10 most frequently selected sensors per condition of this list (see also Figure 5).

The location of the most responsive sensors for each condition and run were expressed in a coordinate system based on each participant's MRI. This allowed us to visually inspect the location and gradiometer direction of the most responsive sensors, superimposed on the participant's MRI. Within individuals, we checked the consistency between runs of the location of the selected sensors for each condition and whether the sensors contained both negative and positive amplitudes, which would indicate adequate coverage of fairly focal generators in the brain between groups of sensors with positive and negative MEG values.

Statistical Analyses

The dependent measures of the analyses were RT to the test pair, latency of the strongest evoked peak, and its absolute amplitude. The data were analyzed as factorial repeated measures designs using linear mixed-effects models (Pinheiro & Bates, 2000). In these models, intraparticipant variability can be estimated from the data and treated as a random factor. Because of this property, they need not assume equal variability across experimental conditions (i.e., the assumption of homoscedasticity in traditional analyses of variance [ANOVAs]). Because these models account for intraparticipant correlation they do not necessarily rely on averaging over conditions within participants to remove these correlations. Furthermore, mixed-effects models can accommodate multiple, nested, random effects and therefore provide a flexible and powerful means of analyzing repeated measures designs (Quene & van den Bergh, 2004; Baayen, Tweedie, & Schreuder, 2002; Cnaan, Laird, & Slasor, 1997). The significance of the fixed effects and their interactions was assessed through ANOVAs using the statistics package R (an open source implementation of the S language, www.r-project.org).

RESULTS

Behavioral Results

The overall error rate was 5.8%. None of the participants showed a speed–accuracy trade-off and error rates were therefore not examined further. We restricted the analysis to same trials because priming effects are typically absent on different trials (Sekuler & Palmer, 1992; Beller, 1971). On a trial, feedback appeared 1000 msec after test pair onset and this limited the upper value of the selected RTs. We analyzed RTs that lay between 250 and 1200 msec on correct same trials where only one button was pressed. The cutoff values affected 0.2% of the otherwise selected trials.

For the RT analysis, the variance of participants and run were modeled as nested random effects to account for each participant's decrease in RT through the experiment. RTs to the test pairs were modeled as a function of three fixed factors. Congruency designated what sequence of figures preceded the test pair, that is baseline (two blank screens replaced the fixation point), control (a square or two patches followed by a congruent composite figure), or experimental (a congruent simple and composite figure). The second factor was Figure Class and could be either cross-shaped or circle-shaped. The last factor was Category and designated whether the figures in the test pair were local, global, or mosaic simple figures.

Congruency affected RT, $F(2,5484) = 25.17, p < .001$; test pairs in the experimental condition were responded to faster than those in the control and baseline conditions (depicted in Figure 3). The effect of Category was significant, $F(2,5484) = 238.35, p < .001$. Mosaic pairs yielded the longest RTs followed by global and local ones. Responses were longer for circle-shaped than cross-shaped test pairs, $F(2,5484) = 27.40, p < .001$,

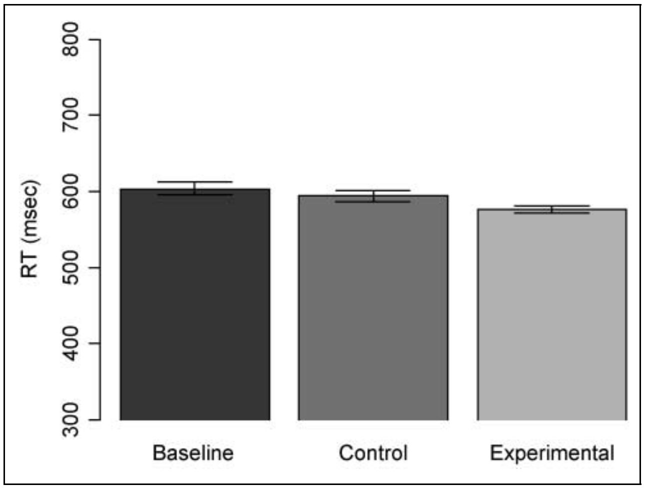

Figure 3. Average RTs and 95% confidence intervals for the different congruency conditions, across Figure Classes (cross-shaped or circle-shaped test pairs) and Categories (global, local, or mosaic test pairs).

and this effect interacted with Category, $F(2,5484) = 25.70$, $p < .001$. Local and mosaic pairs yielded similar RTs for the two figure classes, but global test pairs of the circle-shaped class gave the larger RTs (see Figure 4). This interaction did not differ across levels of congruency. The longer responses to global circle-shaped may have been caused by their similarity to mosaic circle-shaped figures, making decisions on same test pairs containing these figures more difficult than for corresponding global cross-shaped figures. No other effects approached significance, indicating that congruence effects were indistinguishable for global, local, and mosaic pairs.

The main result is that RTs were smallest when both simple and composite figures were congruent to the test pair. More specifically, the RTs in the experimental condition were smaller than when the composite figure was preceded by a control figure. The effect of congruency, therefore, cannot be attributed to featural overlap between the first and second figure or enhanced attention to the location of the composite figure because these properties were present in the control figures as well. Together with our previous behavioral results (Plomp & van Leeuwen, in press) these findings suggest that the simple figures affected processing of the subsequent composite figures.

The congruency effect did not interact with the factors Category or Figure Class. This means that the effect was similar across the types of test pairs and figures used. We may assume that in the experimental condition a simple figure primes the processing of a composite one as either a ''global'' figure lying behind a square, a ''local'' figure lying behind a square or a ''mosaic'' lying next to a square. These priming effects were the subject of subsequent analyses.

The MEG signal analysis focused on the evoked response of the composite figure for different preceding figures. The analysis was therefore restricted to the experimental and control conditions. Differences in latencies and/or amplitudes between the two conditions relate to the effect of congruent versus control primes on the composite figure. Within the experimental condition the evoked response of the composite potentially distinguishes the mosaic from the completion interpretations and could also reveal differences between local and global processing in completion.

MEG Responses

An example of the average MEG signal for one condition within a run is provided in Figure 5. It is obvious from the ''butterfly'' plot that the time-locked response is best captured only by a subset of sensors. We selected these sensors using an objective, data-driven approach (see Methods section). Specifically, we computed for each MEG sensor the SNR in a 20-msec latency range and stepped this window over the full latency range of interest. This way, sensors with the strongest response could be identified for each condition in different runs, revealing a consistent set of strongly responding sensors in 7 out of 10 participants. For the three other participants, the locations of the best responding sensors differed markedly between runs and conditions. This could be either because the signal from these participants was more variable or because the relevant generators were not favorably oriented so that they did not produce currents tangential to the cortex, resulting in a weak MEG signal. These three participants were excluded from the analysis as reported here.[1]

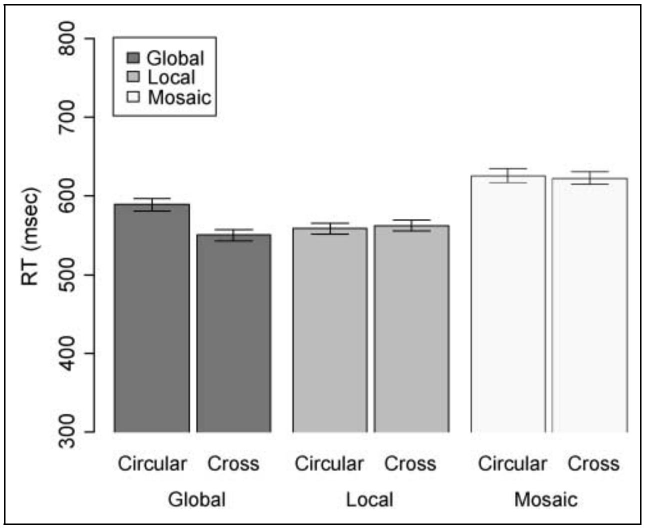

Figure 4. Average RTs and 95% confidence intervals to cross-shaped and circle-shaped test pairs of different Categories. This interaction between Figure Class and Category appeared across levels of Congruency.

From the most responsive sensors we then chose for every condition the 10 sensors that most frequently showed the highest SNR overall. This resulted in the selection of 16 sensors that most consistently responded the strongest to the composite figure. These sensors recorded from occipital ($n = 11$), temporal ($n = 3$), and parietal ($n = 2$) areas of both hemispheres (left, $n = 9$; right, $n = 5$; central, $n = 2$). The mean absolute SNR across the selected sensors was 6.0 (*SD* = 3.4). Changing the selection criterion from 8 to 15 most responsive sensors per condition did not substantially change which sensors were selected.

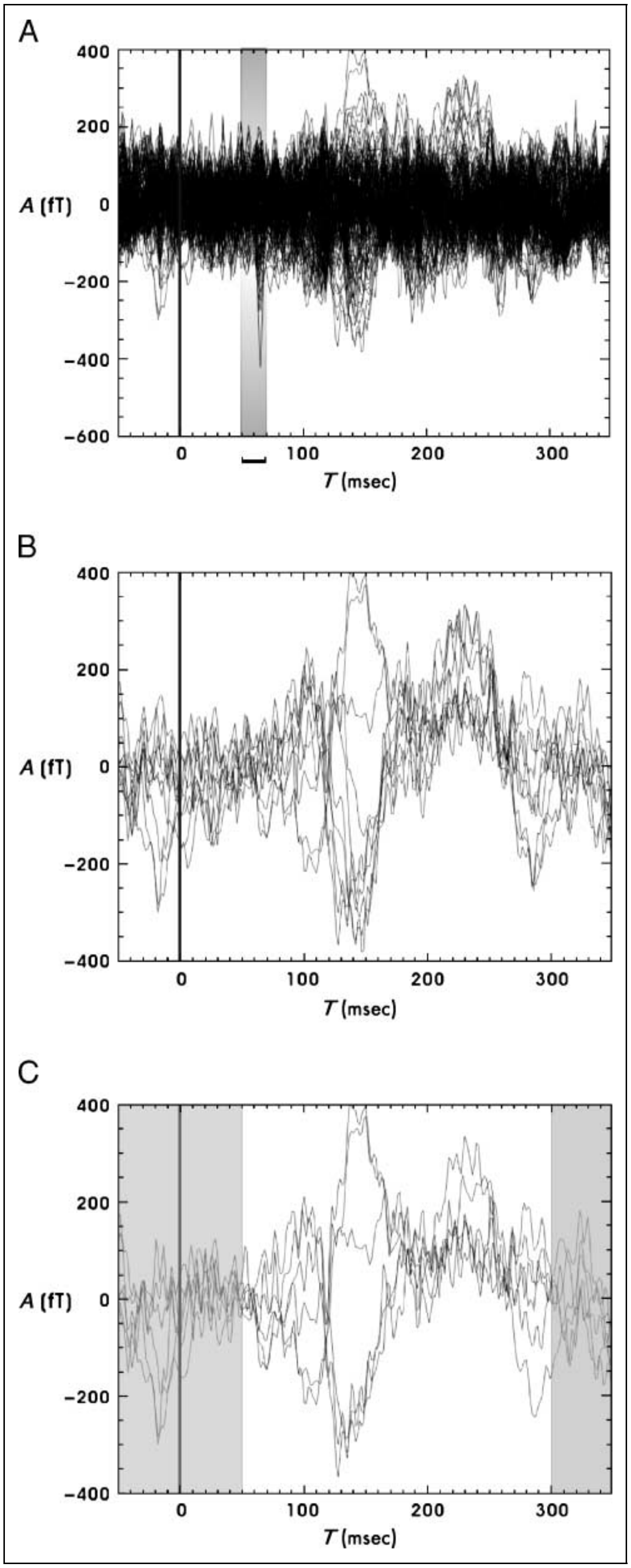

Figure 5. SNR sensor selection. (A) Averaged signal for each of the 151 sensors in a single condition within a run. The solid line indicates onset of the composite figure. The shaded bar depicts the moving window for calculating the SNR at its starting point (see Methods). In (B), only the 10 most responsive sensors, the ones with highest SNRs, are displayed. (C) The subset of these ($n = 6$) that most frequently displayed strong responses to the composite figure. Of these, the amplitude and latency of the largest peak (LP) in the time window from 50 msec after the composite onset to 300 msec afterward (white region) were analyzed.

For the most responsive selected sensors we analyzed the latencies and amplitudes of the largest peak (LP) in the 50- to 300-msec postcomposite interval, for every condition ($n = 8$) within each run ($n = 16$). An exploratory analysis revealed differences in LP latencies and amplitudes between participants as well as between sensors within participants. In the following analyses these two factors were modeled as nested random effects (Pinheiro & Bates, 2000). We first compared the experimental condition (local, global, or mosaic primes) with the control condition (patches and square primes) and then analyzed the differences within these conditions.

Peak Latencies

A first ANOVA assessed the effects of Congruency (control, experimental) on LP latencies of the two Figure Classes (cross-shaped, circle-shaped). The effect of Congruency, $F(1,4903) = 16.60$, $p < .001$, indicated that LP came earlier on experimental (122.7 msec) than on control trials (128.4 msec), depicted in Figure 6A. There was a main effect of Figure Class, $F(1,4903) = 31.77$, $p < .001$, with LP coming earlier for cross-shaped (119.3 msec) than circle-shaped (129.0 msec) composite figures. The two effects did not interact.

Within the control condition the only statistically significant effect was that of Figure Class, $F(1,1144) = 14.72$, $p < .001$, and this was similar to the overall effect. On experimental trials there was an effect of preceding figure (global, local, mosaic), $F(2, 3657) = 4.50$, $p = .01$; global interpretations yielded the latest (125.1 msec) and mosaic ones the earliest LPs (118.9 msec) with local figures (123.9 msec) in between (see Figure 7A). The effect of Figure Class was again evident, $F(1, 3657) = 19.36$, $p < .001$, but did not interact with that of preceding figure.

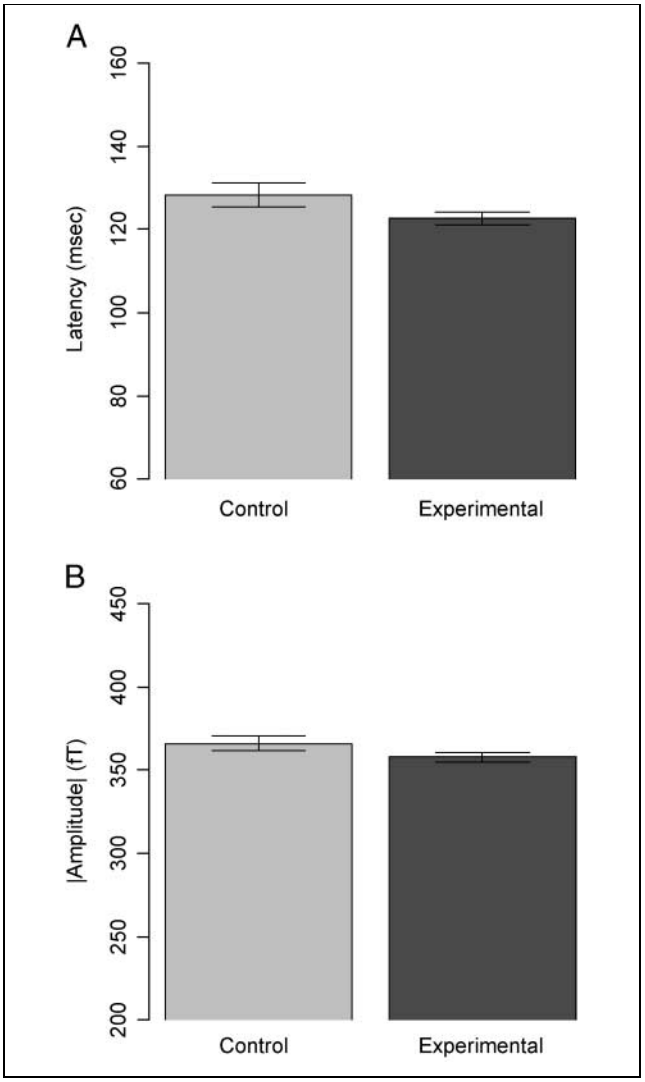

Figure 6. (A) Mean latencies (milliseconds) and (B) absolute amplitudes (femtotesla) of evoked peaks from composite figures in experimental and control conditions. Whiskers represent 95% confidence intervals.

Peak Amplitude

We analyzed the absolute values of LP amplitudes in the same way as the latencies. The different conditions (control, experimental) had an effect on LP amplitude, $F(1,4903) = 19.1, p < .01$; amplitudes in the experimental trials (357.9 fT) decreased relative to control trials (366.2 fT), shown in Figure 6B. There was an effect of Figure Class as well, $F(1,4903) = 66.78$, $p < .001$; amplitudes were larger for the cross-shaped (366.9 fT) than for the circle-shaped figure (353.0 fT).

Within the control conditions the only statistically significant effect was that of Figure Class, $F(1,1382) = 24.15$, $p < .001$; this was similar to the overall effect. In the experimental condition there was an effect of preceding figure (local, global, mosaic), $F(2,3657) = 17.83, p < .001$; when a mosaic interpretation preceded the occluded figure this gave rise to the largest amplitudes (366.8 fT), and when it was a global one they were the smallest (351.0 fT); the amplitudes for local ones (356.4 fT) lay in between (see Figure 7B). The effect of Figure Class was again obtained, $F(1,3657) = 45.79$, $p < .001$, but the two main effects did not interact.

Because of the considerable age range in our participants we checked the data for age-related trends. We found no evidence, however, of a correlation between age and either amplitude or latency of LP, or the differences between experimental conditions.

Anticipation Effect

We chose to balance the design such that within a run the two composite figures had a different control condition, and that this changed over runs. As a result, the unique trials of the control condition only occurred half as often as those of the experimental condition. Seeing the patches, therefore, had, across runs, less predictive power to what stimulus would follow as seeing any of

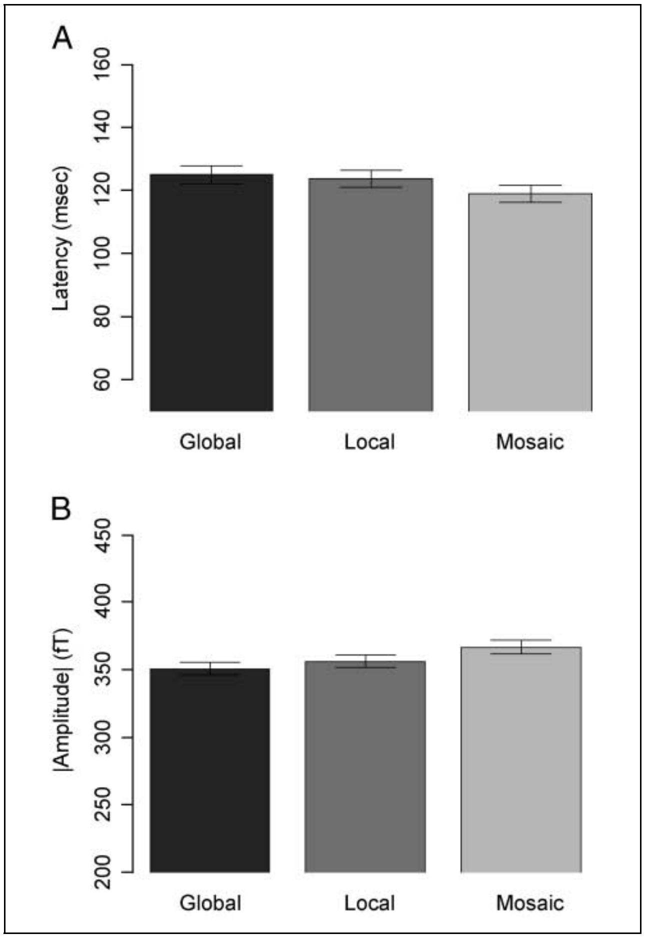

Figure 7. (A) Mean latencies (milliseconds) and (B) absolute amplitudes (femtotesla) of evoked peaks from composite figures when preceded by their global, local, or mosaic interpretation. Whiskers represent 95% confidence intervals.

the simple figures. This difference may have resulted in shorter latencies and smaller amplitudes for experimental trials because on these trials the composite figure could, in principle, be better anticipated. If this is the case, the difference between experimental and control conditions should be smaller for the first than for the later runs because the participant has to learn the contingency as the experiment evolves. Figure 8 depicts the differences between the experimental and control conditions for LP latencies and amplitudes over runs. For both latency and amplitude the deviation of the regression slope from zero is not significant, $F(1,14) = 1.6$ for latencies and $F(1,14) = 1.9$ for amplitudes. The differences between the control and experimental condition can therefore not be explained by anticipatory strategies and may be attributed to characteristics of the preceding figure.

Summary and Discussion

The behavioral results replicated our earlier finding that RTs are smallest when both the simple and composite figures are congruent to the figures in the test pair. In these trials, processing of the composite is facilitated by the simple figure because it corresponds to an interpretation of the composite one (Plomp & van Leeuwen, in press). Our current RT results are in line with this, justifying an analysis of the evoked responses of the composite figures under different priming conditions.

To this extent we selected the sensors that most frequently displayed the highest SNR within a condition. This data-driven approach identified mainly occipital and temporal sensors in both hemispheres, consistent with a complex of generators in the occipital and surrounding ventral and dorsal visual areas that have previously been implicated in amodal completion (Rauschenberger, Liu, Slotnick, & Yantis, 2006; Lerner, Harel, & Malach, 2004; Murray, Foxe, Javitt, & Foxe, 2004; Lerner, Hendler, & Malach, 2002).

Of the composite figures, the cross-shaped one evoked earlier and stronger peaks than the circle-shaped one, irrespective of which figure preceded it (data not depicted). This may be due to differences in the complexity between the two figures. Despite their differences in latency and amplitude, their evoked response changed similarly across conditions. From here on we will focus on the effects of different preceding figures on the evoked response of the same composite figure.

In the experimental conditions, the first figure was always compatible with a possible interpretation (local, global, or mosaic) of the subsequent composite figure. In these conditions, latencies and amplitudes were decreased with respect to the control condition (Figure 6). This is a typical priming effect where the evoked response is attenuated through repeated exposure (Schacter & Buckner, 1998). This congruence effect was observed for average latencies below 130 msec, suggesting that congruent primes affected early perceptual processes. The results, therefore, indicate that alternative interpretations of the composite figure depend on processes taking place in this time frame. Although it is likely that all three interpretations share resources in early vision, the current results do not specify to what degree this may be the case.

Within the experimental conditions, LP latencies and amplitudes differed between primes. When the preceding figure was a mosaic, latencies were shorter and amplitudes larger than for the two occlusion primes, which evoked similar responses (Figure 7). The results, therefore, indicate a distinct effect of the mosaic prime on the early part of the completion process.

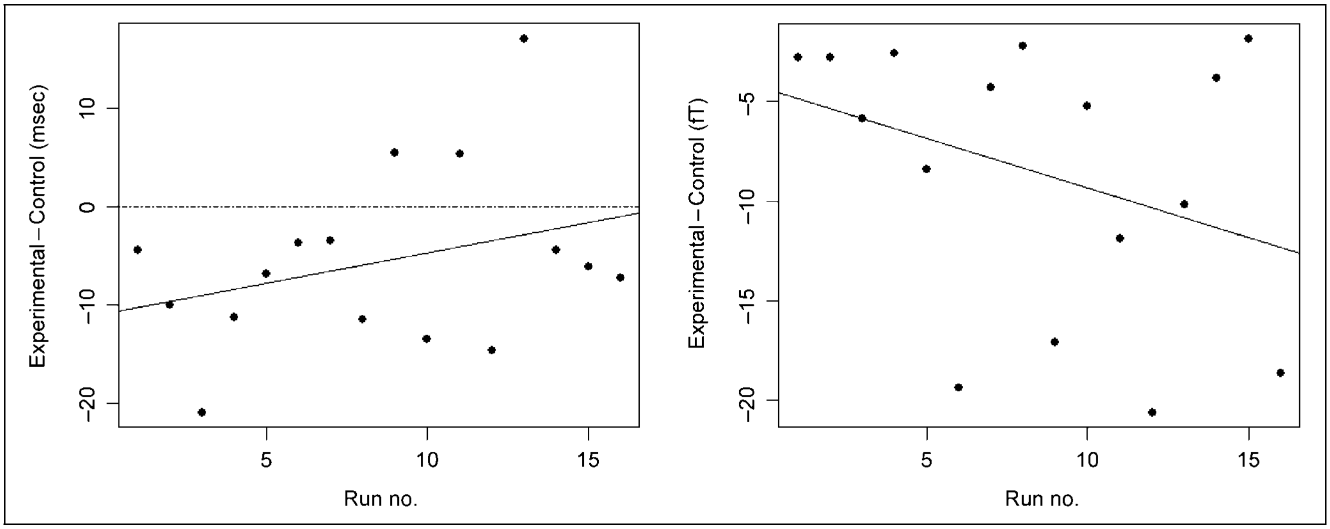

Figure 8. Mean difference in LP latency (left, milliseconds) and amplitude (right, femtotesla) between experimental and control conditions as a function of time in the experiment (in runs).

The latency shift may indicate facilitation of processes preceding LP. The mosaic prime therefore facilitated early visual processes more than the other congruent primes did. We may conclude from these results that there is a time range, before 130 msec, where the processing resembles more that of a mosaic interpretation than that of the completion interpretations. In the present experiment, in other words, mosaic interpretations may be developed simultaneously with occlusion interpretations, but the former finish earlier than the latter. This corroborates recent fMRI work suggesting a progressive representation of composite figures from an image-based feature representation to a completed one (Rauschenberger, Liu, et al., 2006).

Priming generally decreases evoked response (Schacter & Buckner, 1998), but the mosaic prime increased amplitude relative to the other interpretations. In its extreme form, the serial mosaic stage hypothesis would predict that priming the mosaic decreases both latencies and amplitudes for the completion process. The mosaic prime, however, gave rise to processing that is otherwise absent (Henson, 2003). Rather than facilitating a mosaic stage, the processing seems to have been biased toward a mosaic interpretation, resulting in more evoked activity. This would mean that the mosaic prime induced a temporary dominance of the mosaic interpretation that is otherwise absent. Putting it differently, the observed dominance of mosaic interpretations may be restricted to conditions in which the context facilitates them; a mosaic interpretation will not be sustained spontaneously.

It might be argued that overlap in features between prime and composite figure explains the results. Within the control condition the composite could be preceded by two figures, the patches and the square. These figures did not affect LP latency or amplitude, although the latter has substantially more overlap with the composite than the former. Feature overlap, therefore, does not explain the difference between the control and experimental conditions. Within the experimental condition, the explanation does not hold because the mosaic prime increases amplitude, whereas a decrease would be expected based on its greater overlap with the composite.

GENERAL DISCUSSION

Preceding figures affected the evoked MEG signal of ambiguously occluded figures. The effects were observed within 130 msec after stimulus onset. They thus reflect early stages of visual processing. Latencies and amplitudes of the largest peaks (LPs) in evoked activity were smaller when the preceding figure was congruent to one of the possible interpretations of the composite figure. This constitutes a characteristic priming effect. This effect occurred equally with primes for alternative, global and local, completion interpretations and was observed for primes of the mosaic interpretation as well.

Our findings are in line with previous work showing that completion as well as mosaic interpretations of a composite figure can be primed (Plomp & van Leeuwen, in press) and with the idea that the mosaic interpretation is one of many and is computed in parallel (Rauschenberger, Peterson, et al., 2004; Bruno et al., 1997). In particular, RTs to global, local, and mosaic test pairs showed similar congruence effects, and corresponding priming effects were obtained in MEG for global, local, and mosaic interpretations of the composite figures.

The priming results allow for the possibility that mosaic interpretations become dominant in neural activity before occlusion interpretations (Rauschenberger & Yantis, 2001; Sekuler & Palmer, 1992). In this respect, the current MEG results confirm that the mosaic interpretation has a special status. Mosaic primes gave rise to the shortest peak latencies; this means that mosaic interpretations can become available at a faster rate. They could, therefore, dominate occlusion interpretations temporarily. This period would then correspond to a functional mosaic stage in the process of occlusion.

On the other hand, mosaic primes induced the largest amplitudes in the evoked response of composite figures. This observation is inconsistent with the notion of a functional mosaic stage. If a mosaic interpretation would belong to the normal course of events, mosaic primes would result in maximal ease of processing, resulting in the smallest amplitudes, opposite to what we observed. We may, rather, conclude that mosaic primes gave rise to extra processing (Henson, 2003). The increase in amplitude for the mosaic interpretation may lead us to infer that its dominance is context specific. Although most, if not all, of the computation of the mosaic interpretation is mandatory; such an interpretation seems to dominate in early visual processing only when preceding temporal context favors it. Thus, the priming effect in MEG as well as the observed facilitation in responses to mosaic test pairs would not be the result of a context-independent process in which a mosaic gains dominance temporarily. Instead, they would be the consequence of a parallel evolution of global, local, and mosaic interpretations, where the latter only in specific circumstances temporarily dominates the neural signal.

Whether local or global processes control amodal completion has been the subject of considerable debate (Sekuler, 1994; Sekuler, Palmer, & Flynn, 1994; Kellman & Shipley, 1991). We primed both these completions of our composite figures. Although global primes gave rise to the longest latencies and the smallest amplitudes, the current results, however, do not point to very distinctive processing resulting from local and global primes. The differences with mosaic primes were larger than that between local and global ones. The absence of an effect of local and global processing on evoked potentials could be attributed to the fact that they can be processed in similar areas of visual cortex (Kamitani & Shimojo, 2004; Nikolaev & van Leeuwen, 2004; Altmann, Bulthoff, & Kourtzi, 2003).

The latencies of LP in the present study relate to the findings of two recent EEG studies of amodal completion (Murray, Foxe, et al., 2004; Csibra, Davis, & Johnson, 2001). In these studies, completion was associated with activation 140 msec after stimulus onset. This activation originated from lateral occipital regions (LOC), a localization that is supported by two fMRI studies (Lerner, Harel, & Malach, 2004; Lerner, Hendler, & Malach, 2002). The effects we find on LP all precede this interval. The latency shift and the amplitude increase caused by the mosaic prime may thus be related to more elementary processes than those observed in LOC. The presentation of a mosaic prime enhanced early processes more than the presentation of completion interpretations did. This means that the mosaic interpretation is not just one of many interpretations that can be primed early in the completion process. The present result may be regarded as a physiological characterization of the special status of the mosaic interpretation in amodal completion.

The data bear on the question of whether the mosaic stage is a serial or parallel process. In contrast to completion interpretations, the mosaic one can, in principle, result from mere feature segregation and grouping processes. These elementary processes can happen early in the visual stream. In this view, the initial mosaic interpretation resembles a ''full primal sketch'' of grouped image features (Marr, 1982). On such an account, amodal completion can be thought of as at least requiring segregation in depth, that is a 2.5-D sketch of the composite figure. The partly occluded figure can then be amodally completed as a whole lying behind the occluder. Such processes are arrived at with more elaborate processing, presumably involving object-related areas (Lerner, Harel, & Malach, 2004; Murray, Foxe, et al., 2004; Lerner, Hendler, & Malach, 2002).

Our study lends credence to this two-stage view only to a limited degree. Although the mosaic primes shifted latencies by a small amount, the difference was not large enough to maintain that a mosaic stage precedes the completion interpretations in a stepwise, serial manner. Furthermore, the increase in amplitude that they induced is hard to explain as the priming of an initial stage. If there was such a stage then priming it would decrease subsequent activation because less computation was needed to finish the first stage. The opposite result was obtained, suggesting that computation of the alternative interpretations evolves largely in parallel (Bruno et al., 1997), allowing the mosaic interpretation to finish earlier as the result of a favorable spatio-temporal context. Such a parallel account is consistent with previous estimations that completion occurs fast (Murray, Sekuler, & Bennett, 2001; Rensink & Enns, 1998). Completion times can be that fast because completions do not have to wait for a mosaic interpretation to finish.

Our results emphasize that temporal context can set priorities in the completion process so that the mosaic interpretation may become dominant in visual processing, at least for a short period. This explains the results in the literature that have claimed a separate mosaic stage (Rauschenberger & Yantis, 2001; Sekuler & Palmer, 1992). These studies have based their arguments on short exposure times of the target stimuli, in combination with masking. Our present results do not confirm the existence of a serial mosaic stage, but rather that the mosaic is a particular, more rapidly achieved interpretation of an occluded figure that can gain prominence early in perception under a favorable spatiotemporal context.

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Note

1. The analysis including all 10 participants showed, however, the same main effects for latency and amplitude as the analysis for the 7 selected participants.

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