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Cortical responses to contextual influences in amodal completion

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Amodal completion refers to the process in the visual system that enables us to perceive partly occluded objects as whole objects. Both the overall shape of a visual object (global aspect) and the region immediately surrounding the occluder (local aspect) are known to determine the process of completion. We investigated the influence of overall shape context in completion on human brain activity using MEG recordings. Subjects were presented with two different types of shapes that were partly occluded by a rectangle. In the so-called convergent shapes, the local and global contexts trigger the same completion, and in the so-called divergent shapes, local and global contexts trigger different completions. The occluder was removed after 1 s, revealing the whole (completed) shape where expectancies based on the local and global context could either be fulfilled or violated. We found an early (from 200 ms on) left occipital component, which was predominantly sensitive to the figural aspects of the uncovered continuation, but was also modulated by the congruency between the physical shape and the perceived shape (based on the contextual cues). In contrast, an early right occipital component and a later (400 ms) anterior temporal component were sensitive only to the congruency between the physical and the perceived shape, showing the relevance of the global context in amodal completion.

Most objects surrounding us are partly occluded by other objects. However, these partly occluded objects do not result in a percept of fragmented objects; instead, we perceive a world that is made out of wholes. What is even more, we “fill in” the occluded part of an object (e.g., Rauschenberger and Yantis, 2001). This phenomenon, so-called amodal completion, provides us with an illustration of how the brain interprets incoming information from the proximal stimulus. Various properties have been suggested to trigger the generation of completion processes, such as the occurrence of T-junctions (e.g., Rubin, 2001), or the relatability of contours (that is, contours are relatable if the angle between virtual extensions of the occluded shape is equal or greater than 90°, see Kellman and Shipley, 1991). Amodal completion is a fairly fast process; experiments in which priming effects of partly occluded shapes and completely visible shapes are compared have shown that the time it takes to complete simple objects is about 150 ms (Sekuler and Palmer, 1992). Few studies have addressed the issue of neuronal correlates of amodal completion (e.g., Caputo et al., 1999 looked at VEPs induced by texture). Besides the prerequisites for completion, another important issue is the form of a perceived completion. If the requirements for amodal completion are met, the form of the amodal completion can either be determined by the information that is locally available at the intersections between the partly occluded shape and the occluder or by the global context that takes into account the overall structure of the partly occluded shape. Although psychophysical evidence has been found for the relevance of both influences (e.g., Sekuler, 1994; Tse, 1999; Van Lier et al., 1994, 1995a,b), the role of global context in amodal completion is still underestimated. In this experiment, we seek further converging evidence for global contextual influences by measuring brain potentials.

To illustrate the issue of contextual influences in amodal completion, take for example the partly occluded shape in Fig. 1A. If the completion is just based on local context, the completion typically comprises a linear or smooth continuation of the occluded contours as shown in Fig. 1B (e.g., Kellman and Shipley, 1991; Fantoni and Gerbino, 2003; Singh, 2004). If the completion is based on global context, the completed part typically builds upon the regularity of the visible part, as shown in Fig. 1C, where regularities include figural properties such as symmetry and iteration. The latter is actually shown to be the

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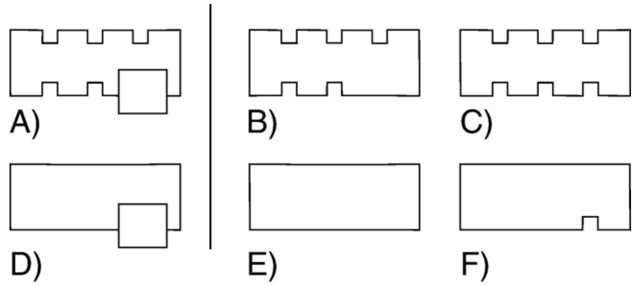

Fig. 1. (A) A divergent partly occluded shape. (B) A local contextually dependent (linear) completed form of the divergent shape. (C) A global contextually dependent (indentation) completed form of the divergent shape. (D) A convergent partly occluded shape. (E) A linearly completed form of the convergent shape, note that this is triggered by both global and local context. (F) An indentation completed form of the convergent shape.

dominating completion for these kinds of (regular) stimuli (e.g., Sekuler, 1994; Sekuler et al., 1994; Van Lier, 1999, 2001; Van Lier and Wagemans, 1999; De Wit and Van Lier, 2002; De Wit et al., 2005a,b).

As noted, the influence of global context depends on the figural aspects (regularity) of the partly occluded shape. In the present experiment, there were two different types of shapes. For both types, the local context at points of occlusion was the same, whereas the global context was different. In the so-called divergent shapes, local and global context triggered different completions (local context resulting in a linear completion and global context resulting in an indentation, see Figs. 1A, B, C). In the so-called convergent shapes, the local and global context triggered the same, linear completion (see Figs. 1D, E, F). In the experiment, the subjects first viewed a partly occluded shape. After 1 s, the occluder was removed, revealing the whole (completed) shape, where expectancies based on context could either be fulfilled or violated. That is, the presented physical completion could correspond to the experienced (plausible) completion or it could be a different (less plausible) completion (as shown in a simple drawing task and primed-matching tasks, e.g., De Wit and Van Lier, 2002).

To investigate the neural responses associated with the congruency between physical and perceived completions, we measured MEG and time-locked the analysis of event-related fields (ERF) to the time-point of the removal of the occluder. The only task for the subjects was to observe the whole cycle of these shapes being partly occluded and appearing in its totality. We hypothesized that, similar to the mismatch negativity found for deviant stimuli in the auditory and visual domain (Näätänen, 1991; Tales et al., 1999), the implausible (surprising) physical completion should result in larger neural responses compared to a plausible (expected) completion. For the divergent shapes, absence of an indentation would violate expectancies induced by the global context. For the convergent shapes, the linear completion is the most plausible or least surprising solution, and the occurrence of an indentation is the most surprising completion as the indentation violates expectancies based on both global and local contexts. Compared to this, the divergent shape is more ambiguous, and therefore a smaller surprise effect is expected for the linear (local) continuation for the divergent shapes as compared to the indentation for the convergent shapes.

Materials and methods

Subjects

Magnetic evoked fields were recorded from nine subjects (4 male and 5 female, 23–33 years old, mean age: 26). All subjects were in good health with no history of neurological or psychiatric disorders and gave informed written consent. All had normal or corrected-to-normal vision.

Stimuli and procedure

Six sets of stimuli were used, based on the following shapes: a square, a rectangle, an isosceles triangle, an equilateral triangle, a pentagon, and an octagon. For each of these sets, there were three rotated versions. To create different contextual cues to induce different completions, shapes were either perfectly linear, convergent shapes, or had indentations in the visible part of the partly occluded shapes, divergent shapes. Different continuations consisted either of a linear extension or an indentation (similar to the shapes manipulated in Fig. 1). This all resulted in 6 (sets) × 3 (rotations) × 2 (sort of overall shape: divergent vs. convergent) × 2 (sort of continuation: linear vs. indentation) = 72 different stimuli. These were repeated in ten blocks, thus resulting in 720/4 = 180 trials per surprise/no-surprise condition. The visual angle of the total shape was 12°. The occluder (a small square) was always placed in the lower right part of the shape. In all screens, a fixation cross was shown in the center of the screen to keep subjects' eyes fixated at the center of the screen, and the shapes were always white on a black background.

Prior to the experiment, electrodes and localization coils were attached (see below). Subjects sat comfortably in a dimly lit room with their head approximately 2 m from the screen and passively viewed the trials. Each trial consisted of the following time structure: first, only the fixation cross was shown for 1 s, then the occluded shape was shown for 1 s, followed by the shape without the occluder, revealing a continuation, also shown for 1 s. After each block of 72 trials, a 1-minute break was given, using a dark gray screen for 50 s, followed by a lighter gray screen for 10 s, which signaled the start of another block of trials. Subjects were instructed only to blink during the initial 1 s presentation of the fixation cross in each trial. Stimuli were run using Presentation© (Neurobehavioral Systems, Inc., Albany, CA, United States). The recording session consisted of approximately 45 min of pure recording time. After the recording session, structural MRIs of each individual subject were obtained on a 1.5 T SIEMENS Sonata scanner (Siemens, Erlangen, Germany) in order to enable later source analysis (not presented here) and to allow the data to be interpolated on a standard helmet template.

Recording

Evoked fields were measured using a 151 channel axial-gradiometer whole-head MEG system (Omega 2000, CTF Systems, Vancouver, Canada) in a magnetically shielded room. Data were recorded with a sampling rate of 1200 Hz using an anti-aliasing filter with a cutoff frequency at 400 Hz in 720 epochs of 1000 ms (200 ms before occluder disappeared, until 800 ms after this critical event; 200 ms pre-stimulus period). Prior to MEG measurements, each subject was fitted with three coils that were placed at the nasion and the left and right preauricular points in order to localize the position of the head of the subject relative to the MEG sensors before and after the session. Horizontal and vertical EOG was registered with three electrodes.

Data analysis

Data were analyzed using the Fieldtrip software package (see for more details http://www.ru.nl/fcdonders/fieldtrip), a MATLAB-based toolbox for electrophysiological data that has been developed by our group. Line noise removal was performed by estimating the amplitude and phase of the 50 Hz line frequency component in a 10-second piece of data around each epoch of interest and subsequent subtraction of this component from the data. Data were checked for artefacts using a semi-automatized artefact routine that checks for eye-blinks, muscle artefacts, and sudden jumps in the signal caused by the SQUID-electronics. For each of these artefacts, a statistical threshold for rejecting periods that exceeded this threshold could be iteratively set by the user for the complete data set of each individual subject. Adjustments to individual subjects' data were necessary because of different noise levels, differences in eye-blink frequency, and amplitude. A similar semi-automatized artefact routine was used to detect squid-jump artefacts and muscle artefacts. To allow grand averaging of the MEG data over all subjects, we compensated for the fact that subjects have different head positions with regard to the sensor array by realigning the data to a common sensor array template using a procedure that is based on a minimum norm projection (Knösche, 2002) and incorporates information about subjects' head position and shape. Data were low-pass-filtered (cutoff frequency set to 40 Hz), and jackknife averages were computed for each condition. Realignment was done on these jackknife repetitions. and planar gradiometers were computed using a nearest-neighbor method. The main interest of this study was to investigate how different physical completions would affect brain activity and how this would depend on the global figural context. In order to test for significant differences between the main experimental conditions (the different physical completions–linear continuation and indentation–for the convergent and the divergent shape), a paired t test was calculated for the individual samples of a time-domain moving average of the evoked fields. The moving average was calculated over a symmetrical window of 20 samples corresponding to a 16 ms interval. This revealed times of interest and regions of interest that roughly corresponded to the most apparent spatio-temporal clusters of differential activity between individual conditions. To test for the differential effect of the physical completions in the different shapes, a double difference wave was computed in the following way: $[\text{Convergent}_{\text{indentation}} - \text{Convergent}_{\text{linear continuation}}] - [\text{Divergent}_{\text{indentation}} - \text{Divergent}_{\text{linear continuation}}]$, therefore assessing the differential effect of an indentation as a local feature under different global shapes. Such a differential effect is best captured in the interaction term of an ANOVA type of analysis. Therefore, we computed a 2 × 2 repeated measurement ANOVA with factors "Global shape" (with two levels: "Convergent" and "Divergent") and "Local feature" ("Indentation" and "Linear Continuation") in regions and time intervals of interest (see Results section). The main effects are of little interest here since they are a redundant to the running t tests computed over the four conditions (with a different way of combining the conditions), the interaction, however, is of main interest. Deviation from sphericity of the error-covariance matrix was assessed by Mauchly's test of sphericity. No deviation from sphericity was found.

Results

All results are shown using grand-averaged planar gradients, a metric that usually shows the maximum of neuromagnetic activity in sensors that are overlying its cortical origin (Bastiaansen and Knösche, 2000) and is positive, irrespective of the orientation of its underlying dipole. Evoked fields were calculated with respect to the removal of the occluder as the stimulus "onset" and baseline were calculated immediately prior to this event (−100 ms to stimulus onset). Thus, the evoked fields, as reported here, reflect the brain's response to the stimulus change in the right lower quadrant and should not be influenced by the global shape of the figure (convergent vs. divergent) per se (since these have remained stationary on screen for 1 s). In Fig. 2, the evoked responses to the disclosure of the convergent shapes are shown, where the green line indicates the response to the linear continuation and the red line indicates the indentation continuation. The figure shows the topographically arranged overview of individual sensors, and additionally the timecourses of selected regions of interest are outlined in further detail. Activity starts to rise over occipital cortex as early as 100 ms, being strongly lateralized in favor of contralateral (left) occipital cortex, and then extends into more anterior regions, also covering sensors overlying right temporal cortex. Activity in these sensors most likely corresponds to higher level visual areas (of the ventral stream) in the temporal lobe. Fig. 2 furthermore shows that activity is largely restricted to occipital and presumably inferior temporal areas while sparing parietal, central (sensorimotor), and frontal areas. This is explained by the fact that subjects were passively viewing stimuli, and furthermore it shows the spatial selectivity of planar gradients as the metric chosen here.

It can be seen that there is an early large difference between the two physical completions, such that the indentation–continuation evoked larger responses in several regions, including left and right occipital as well as left and right temporal regions (at somewhat later time-points). These differences will be described in more detail below.

In Fig. 3, average responses for the divergent shape are shown, where the green line again depicts the linear continuation and the red line depicts the indentation. The overall activity pattern for the divergent shape is similar to the convergent shapes; the early evoked brain responses in left occipital and temporal cortex to the indentation are larger than the response to the linear continuation (see for example also the left occipital channel Locc). However, looking at right anterior temporal channels, these show an inverse pattern at later time-points: an indentation continuation here leads to a smaller amplitude of the evoked response than a linear continuation.

Thus, the results show that removal of the occluder results in a physiologically meaningful pattern of evoked brain activity, spreading from contralateral occipital cortex along the ventral stream to higher level areas including anterior temporal regions. Furthermore, disclosure of different shapes leads to differential patterns of visual evoked fields. Below, we investigate these differential effects more systematically.

Effect of an indentation in the convergent shape

Fig. 4 shows the difference waves for the contrast "indentation against linear continuation" for the convergent shape. In this contrast, occurrence of an indentation violates expectations based on both local and global context. The red lines in the timecourses

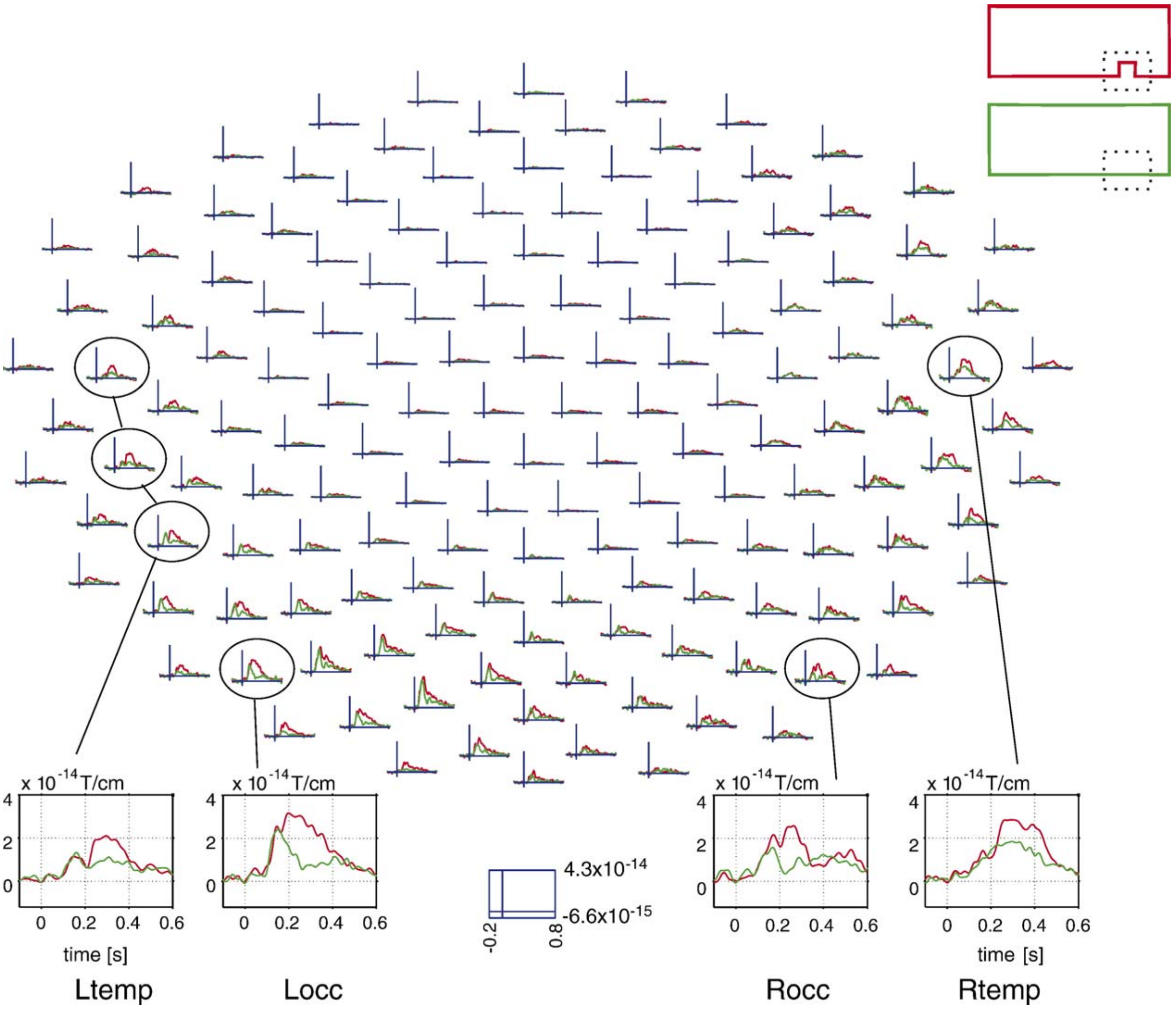

Fig. 2. The planar gradients (fT) over the whole brain averaged for the convergent shape over the nine subjects from 100 ms before, until 600 ms after occluder removal. The red line is the activity for the physical linear continuation and the green line for the indentation. Also zooming into left and right occipital (Locc and Rocc) and left and right temporal (Ltemp and Rtemp) sensors.

of Fig. 4 reflect periods where there is a statistically significant ($P < 0.01$) difference between indentation and linear continuaxtion. Statistical significance was assessed by means of a paired t test calculated over a moving average of the evoked fields in both conditions. An early deflection of the difference wave has a topography (see upper topography of Fig. 4, averaged between 180 and 250 ms) that reveals three components (as identified by their spatial peaks and different timecourses): a medial and two lateral occipital ones (left and right). The topography of the left medial source is in good agreement with previously observed topographies from V1 sources (e.g., Hoogenboom et al., 2006), even though this remains speculative. Statistical significance is reached from approximately 160 ms to 250 ms for the medial and the right occipital components (200 ms to 360 ms for left lateral–occipital component). The strongest increase for indentation is observed approximately 260 ms after removal of the occluder in the left lateral occipital component which is also the dominating source of the evoked response to the removal of the occluder. Differential activity is then also observed further along the left ventral stream in sensors overlying temporal areas and reaches a stable plateau lasting from approximately 240 ms to 360 ms (see middle topography of Fig. 4, averaged between 320 and 360 ms). Finally, differential activity emerges in right temporal sources from approximately 250 ms on and peaks at approximately 430 ms. Statistical significance is reached at approximately 320 ms after stimulus onset, and the difference disappears around 500 ms (see lower topography of Fig. 4, averaged between 400 and 450 ms). Activity in both right and left temporal sensors is very likely reflecting activity in more anterior temporal visual areas, and therefore higher level areas of the ventral visual stream.

Effect of an indentation in the divergent shape

Fig. 5 shows the same difference waves as Fig. 4 for the divergent shape. In this contrast, occurrence of an indentation violates expectations based on local context, but it is in agreement with the global context. Occurrence of a linear continuation in turn harmonizes with the local context but violates the expectations based on global context. The early topography reveals a similar pattern of enhanced amplitudes over medial and left occipital regions for the indentation continuation. The medial source shows early enhanced response peaks for the indentation from around 100

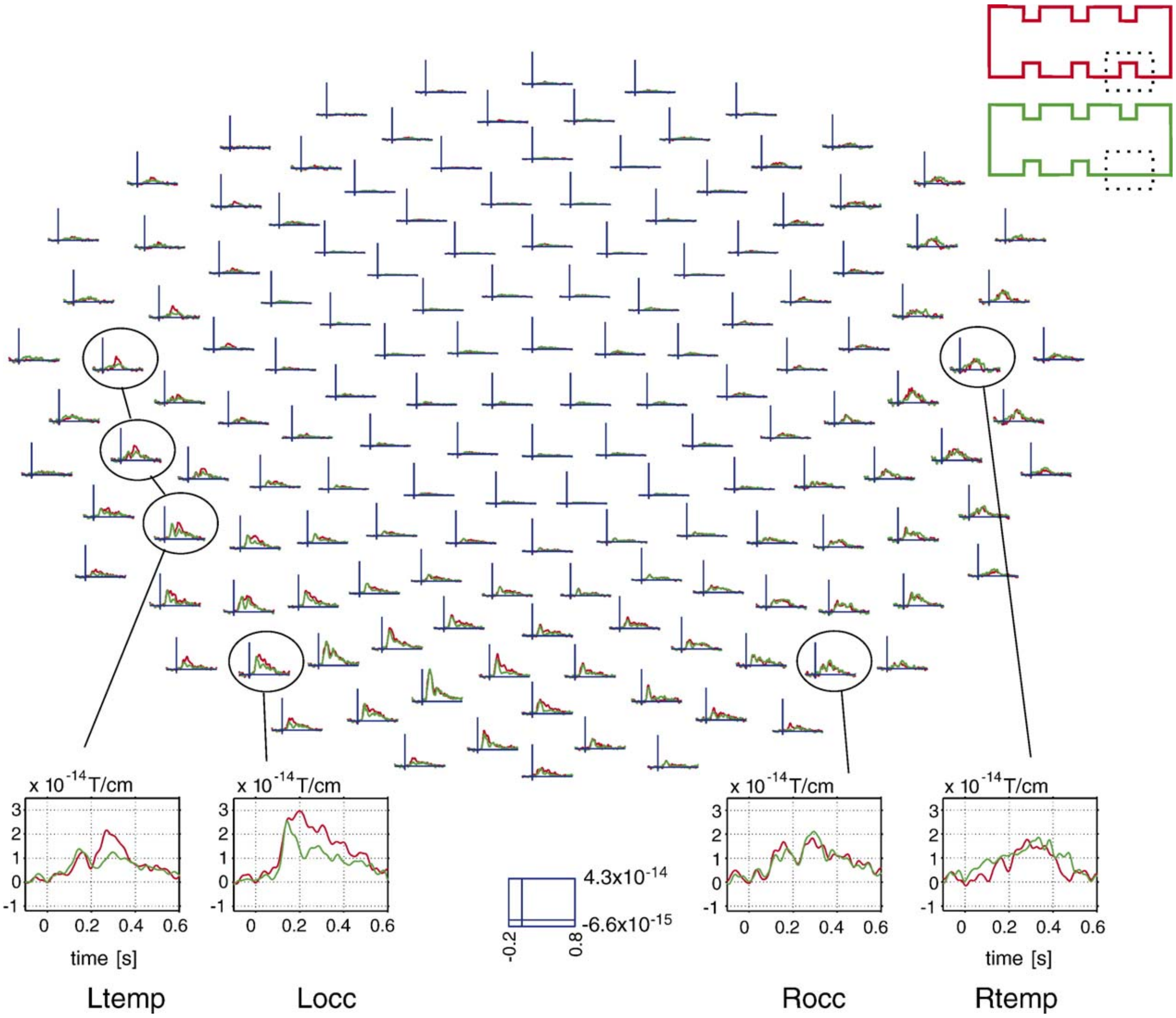

Fig. 3. The planar gradients (fT) over the whole brain averaged for the divergent shape over the nine subjects from 100 ms before, until 600 ms after occluder removal. The red line is the activity for the linear continuation and the green line for the indentation. Also zooming into left and right occipital (Locc and Rocc) and left and right temporal (Ltemp and Rtemp) sensors.

ms on, but these very early effects are not statistically significant. Statistical significance is reached from 240 ms to 330 ms, when the difference wave reaches a stable plateau (upper topography in Fig. 5, averaged between 180 and 230 ms). The strongest increase for indentation is observed approximately 200 ms after removal of the occluder again in the left lateral occipital source. Overall, the amplitude differences here appear to be reduced compared to the convergent shape. Furthermore, in striking contrast to the convergent shape, there is no sign of differential activity in right occipital regions, which was a dominant feature of the difference wave for the convergent shape. Differential activity is also observed over left temporal sensors between 230 ms and 350 ms (statistical significance is reached between 270 and 350 ms; middle topography in Fig. 5, averaged between 240 and 300 ms), similarly to the convergent shape. Remarkably, starting from around 420 ms on, occurrence of an indentation actually leads to a significantly *reduced* activation level over extended right temporal areas, when compared to the linear continuation (bottom topography in Fig. 5, averaged between 460 and 480 ms). This late decrease peaks around 470 ms and disappears around 500 ms.

The differential effect of indentation for divergent versus convergent shapes

The comparison of the difference waves for the divergent versus convergent shapes revealed clear distinctions. In order to test these more explicitly, a 2 × 2 ANOVA with factors “Overall shape” and “Indentation” was calculated over the mean amplitudes in time intervals (TOI) and regions of interest (ROI, as indicated in Fig. 6). The outcome of such an interaction is closely related to a subtraction of the difference waves for convergent and divergent shapes ([$\text{Convergent}_{\text{indentation}}$ + $\text{Divergent}_{\text{linear continuation}}$] − [($\text{Divergent}_{\text{identention}}$ + $\text{Convergent}_{\text{linear continuation}}$]), and the results of both are shown in Fig. 6. In the early interval (between 230 and 280 ms, see upper topography), the left and right lateral occipital components dominated the topography and in both ROIs the interaction was significant ($F = 11.74$, $P = 0.009$ for left occipital; $F = 11.805$, $P = 0.009$ for right occipital). The main effect of “Indentation” was also significant, as to be expected from the running t statistics. Not significant was the effect of “Overall shape” ($F = 0.008$, $P = 0.93$, left; $F = 0.001$, $P = 0.98$, right) which confirms that this has no influence per se on the evoked fields

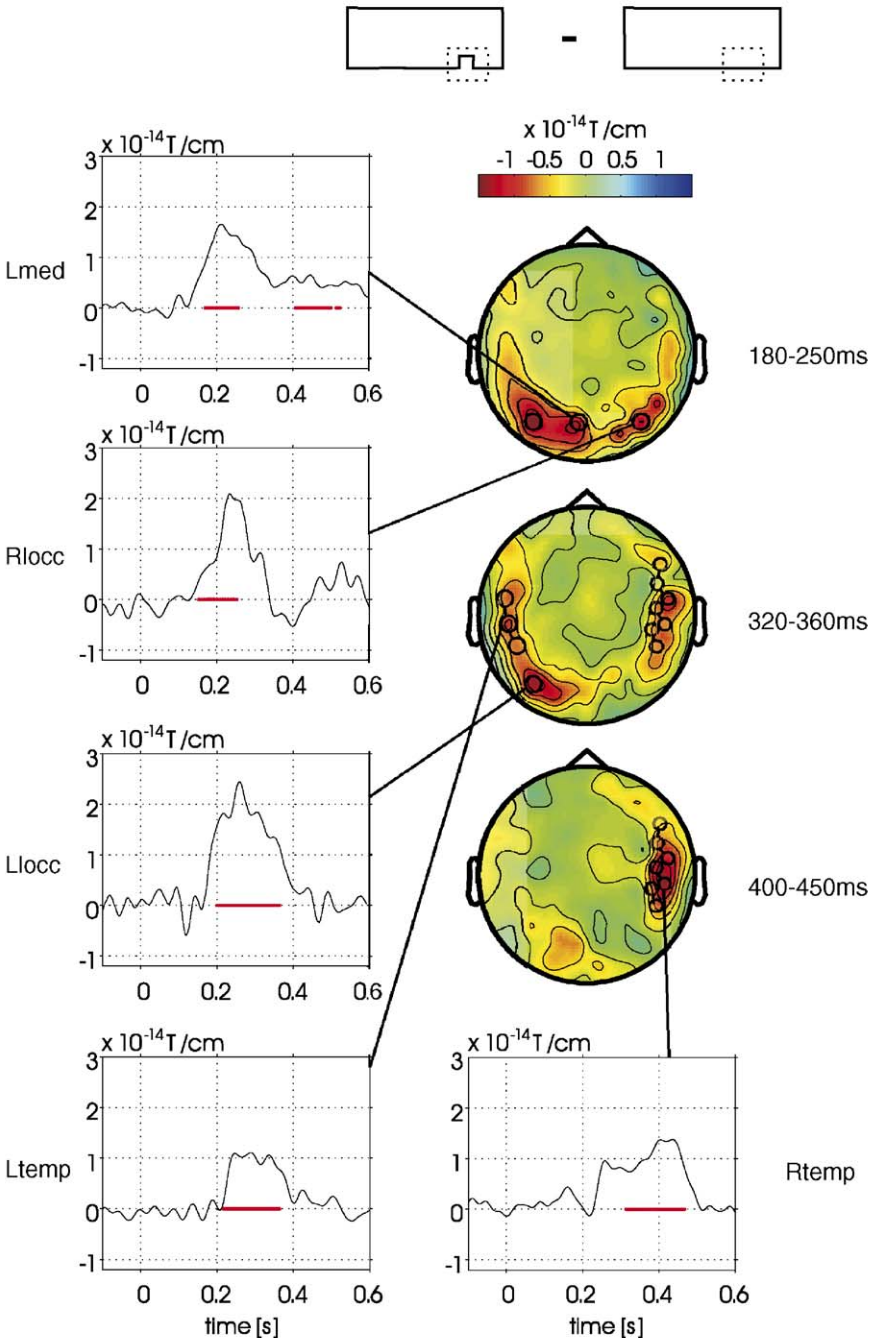

Fig. 4. Difference waves for the contrast indentation against linear continuation for convergent shapes, where red lines indicate timecourses with a statistically significant difference ($P < 0.01$). In addition, three topographies are shown for this difference: the upper showing a medial, a left, and a right occipital component (Lmed, Llocc, and Rlocc, averaged between 180 and 250 ms). The middle topography showing some left ventral components (Ltemp, averaged between 320 and 360 ms), and finally the lower topography shows a right temporal component (Rtemp, averaged between 400 and 450 ms).

triggered by the removal of the occluder. The ANOVA was also calculated for an ROI in the left temporal cortex in a TOI where the difference wave reached its maximum, but the interaction did not approach significance ($F = 1.33$, $P = 0.28$). Finally, the interaction was tested over right temporal cortex in a narrow TOI between 450 and 460 ms, which was also found to be highly significant ($F = 11.568$, $P = 0.009$, see also lower topography).

Even though the result of the ANOVA and the double difference are similar for the three components–such that evoked responses have greater amplitudes for the indentation continuation in the convergent shape – the underlying pattern is different in three respects. Firstly, the left occipital (contralateral) component is always enhanced by the indentation continuation, but the strength of this modulation furthermore depends on the global context of the shape. Thus, although violation of the local cue seems to be the dominant factor, activity of this component is nevertheless modulated by the congruency of the stimulus with the global context. Secondly, and in contrast to the left occipital component,

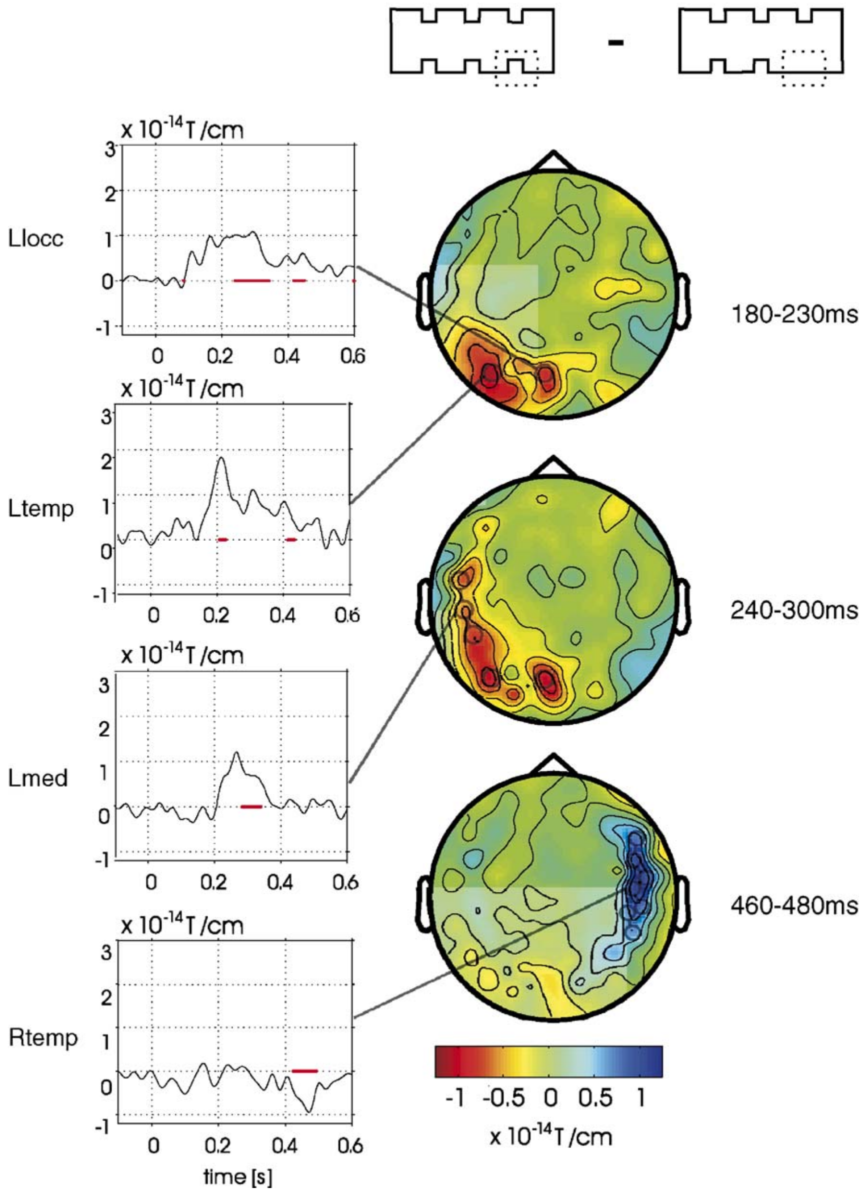

Fig. 5. Difference waves for the contrast indentation against linear continuation for divergent shapes, where red lines indicate timecourses with a statistically significant difference ($P < 0.01$). In addition, three topographies are shown for this difference: the upper showing a left medial and a left lateral occipital component (Lmed and Llocc, averaged between 180 and 230 ms). The middle topography showing some left ventral components (Ltemp, averaged between 240 and 300 ms), and finally the lower topography shows a decrease in a right temporal component (Rtemp, averaged between 460 and 480 ms).

activity in the right occipital source is equally strong for indentation and linear continuation for the divergent shape, but it is strongly enhanced by the occurrence of an indentation in the convergent shape. In other words, incongruency with local cues alone does not seem to affect this component, violation of the expectancies based on global context seems to be a necessary condition to modulate this source. The idea that this component reflects processes that deal with integration of parts of the shape into the global context is further supported by another comparison investigating the effect of global context: comparing the linear continuation of the convergent shape (Fig. 2) with the linear continuation of the divergent shape (Fig. 3) reveals brain responses to the violation of global expectations, with the same physical stimulus behind the occluder. Supplementary Fig. 1 shows the difference wave of the right occipital source for this comparison. The evoked field shows a clearly enhanced amplitude for the incongruency of the linear continuation with global shape properties, with a very similar timecourse as observed in the contrast for indentation vs. linear continuation in the convergent shape. Together, the results therefore indeed suggest that this source is sensitive to the relation of the physical continuation with the global shape while being less sensitive to the physical stimulus aspects. Finally, the third different pattern in the right temporal region shows a double dissociation of the effect of indentation for the different global shapes: whereas indentation leads to a strongly enhanced response in the context of the convergent shape (where both local and global cues suggest the linear continuation), occurrence of an indentation leads to a reduced activity (compared to linear continuation) for the divergent shape,

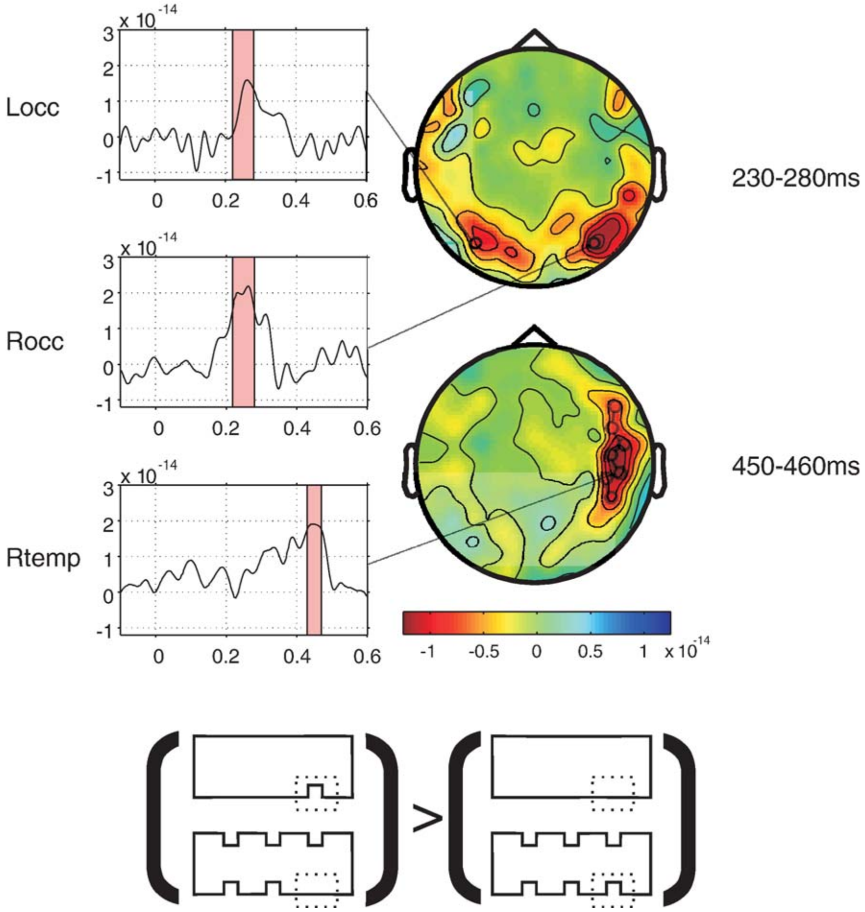

Fig. 6. Double difference waves for the interaction between indentation and linear continuation for both shapes (closely related to [Convergent$_{\text{indentation}}$ − Convergent$_{\text{linear continuation}}$ −] − [Divergent$_{\text{indentation}}$ − Divergent$_{\text{linear continuation}}$]), where red areas indicate timecourses with a statistically significant difference ($P < 0.01$). In addition, two topographies are shown for this double difference: the upper showing the left and right lateral occipital components (Llocc and Rlocc, averaged between 230 and 280ms) and the lower showing the right temporal component (Rtemp, averaged between 450 and 460ms).

where global cues are in agreement with the occurrence of an indentation, but local cues are not. That is, the sign of the effect of an indentation depends on its consistency with the global aspects of the presented shape.

Discussion

In this study, we investigated brain responses that are evoked by the removal of a rectangle that partially occluded a shape. Seeing these partly occluded shapes, that had two globally different forms, could give rise to a percept of a completed object, influenced by both the local and the global context. The hypothesis was that violation of these percepts would modulate distinct components of visual evoked fields and would therefore provide insight into the neural machinery governing local and global influences in amodal completion. The results show that different physical completions indeed caused differential brain responses that depended on the integration of the physical completion into the figural context.

Firstly, the occurrence of a physical indentation after the removal of the occluder in general resulted in an increased amplitude in left occipital cortex, contralateral to the indentation, after approximately 200 ms when compared to the condition where no physical indentation was present. The difference between these conditions can therefore in principle be attributed to both the higher structural complexity of the indentation compared to the linear continuation, as well as the inconsistency of this shape with the results of the local and global context. However, this early left component was even stronger when the indentation was incongruent with the overall shape, suggesting that this component is sensitive to both local and global context. Since the occurrence of the indentation seems to overwrite the consistency with the global context, we think that this component is more sensitive to the complexity of the physical completion per se, and less to the contextual relations. The enhanced activity for the occurrence of an indentation, independent of its congruency to global attributes, prevails in left temporal regions, presumably reflecting activity of higher visual areas in the ventral stream. While the occurrence of an indentation was also the driving force for this component, suggesting that it is primarily sensitive to the physical completion, the amplitude of its response is also modulated by the integration of local cues into the global context of the shape.

Secondly, a different pattern appeared in sensors overlying the right occipital cortex. The pattern found here was more complicated. Occurrence of an indentation per se did not consistently affect these sources in the same direction for the different shapes. The right occipital component showed early differential activity, where enhanced responses were observed when an indentation violated both local and global context (convergent shape), but no significant difference was found when an indentation was congruent with the global context (divergent shape). However, violation of global context by a linear continuation in the divergent figure caused increased activity compared to the same linear continuation for the convergent shape (when this was in congruence with local and global cues). Together, this suggests that the right occipital region is sensitive to the integration into a global context, independent of the local features per se.

Thirdly, a final distinct pattern appeared in the right temporal cortex: the sign of the effect of an indentation here depends on its congruency with the global context. When the occurrence of an indentation violates the global context, a strongly increased amplitude of the evoked field is observed (convergent shape, Figs. 1 and 3). The effect is very late, starting around 300 ms and having a peak latency of approximately 430 ms. If the occurrence of an indentation is congruent with the global aspects of the shape, this effect is reversed. Thus, the linear continuation evokes a stronger response, even though reduced in amplitude and with a slightly different timecourse (peak latency ~470 ms). Interestingly, this source did not show significant differential activity in the contrast Divergent linear continuation vs. Convergent linear continuation, as calculated for the right occipital component. These findings suggest that at this level local and global contextual processes interact. Violation of local context always affects this source, but the size of this effect strongly depends on the congruency of the physical completion with the overall shape. In that sense, the pattern is somehow reversed with respect to the behavior of the left occipital component: global context dominates (in that they control how physical completions act on this source), but activity still depends on the local context.

Overall, our results fit in with results from an ERP study by Johnson and Olshausen (2003) on object recognition, which showed earliest components that reflected low-level feature differences between images, whereas later components (150 ms–300 ms) were related to recognition of objects and the duration of this component co-varied with accompanying RT. Similarly, in our experiment, the earliest components were primarily responsive to the lower-level physical stimulus attributes, the latter being more strongly affected by the integration of these into the global object context. Furthermore, the enhanced amplitudes we find for the unexpected physical completions are in agreement with an enhanced negativity for unexpected stimuli (after 250–400 ms) over occipital and temporal electrodes found in a visual mismatch experiment by Tales et al. (1999). This component was also associated with the rarity of the deviants and not the physical features distinguishing them from the standards.

A candidate source for our lateral occipital components is the LOC; an fMRI study by Kourtzi and Kanwisher (2001) showed that the lateral occipital complex (LOC) represents perceived shapes and not contours per se. In fact, in a more recent study, Altmann et al. (2004) show that context (defined as the background elements) modulates activity in the LOC, depending on the relevance for the foreground shape. Our right occipital component is shown to be primarily related to the contextual integrity of the presented shapes.

On a more abstract level, particularly our late right temporal component may reflect some non-linguistic counterpart to the N400, a component that is triggered by visually or auditorily presented words that are semantically incongruent with the rest of the sentence (e.g., Kutas and Hillyard, 1980; Van den Brink et al., 2001). The late right temporal component also responded to violations of global context with an enhanced amplitude, independent of the physical shape of the completion, and its timing is somewhat similar to the N400. In a spoken-word recognition experiment by Van den Brink et al. (2001), subjects were presented with sentences in which the last word either was congruent, semantically anomalous, but with the same initial phonemes as the congruent words, or semantically anomalous and with a different beginning compared to the congruent word. An N200 effect was found for words that were both semantically anomalous and for which the beginning of the last word differed from the congruent last word. In addition, an N400 effect was found if the last word in the sentence was semantically anomalous. Thus, the sequence of effects is similar to those found in our study. Whereas little is known about the neural generators of the N400 as found in linguistic experiments, the planar gradient topography of the right temporal component suggests an origin in more anterior temporal areas (and therefore higher visual areas of the ventral stream) since the sensors, where this component is measured, are overlying the more anterior part of temporal cortex. All in all, these studies show the relevance of contextual information in different modalities and their effects on various brain responses. As mentioned earlier, contextual effects were shown in the formation of amodal completions, using psychophysical methods such as the primed-matching paradigm (e.g., Sekuler, 1994; De Wit and Van Lier, 2002). The data presented here can be regarded as the first neurophysiological data that support the formation of local and global completions, depending on the context. Note, however, that the results do not reveal information on the microgenesis of amodal completion itself as our data were obtained 1 s after the partly occluded shape was shown.

The hemispheric asymmetries we find agree with several studies suggesting a hemispheric specialization of the processing of local versus global stimulus aspects, the left hemisphere being dominant for local processing, whereas the right hemisphere (primarily occipital and occipito-temporal regions) has been found to be specialized in the processing of global stimulus attributes (e.g., Robertson and Lamb, 1991; Fink et al., 1997; Heinze et al., 1998). In principle, the lateralization of local and global effects in the left and right hemisphere in this study may be related to the lateralized position of the occluder (and therefore the physical completion) in the right hemifield. Although the contralaterally found dominance for local cues (low-level visual features) may in principle be explainable by the fact that activation of early visual areas is constrained to the contralateral hemisphere, the differential behavior at the level of higher level areas, in particular temporal regions (with large receptive fields), is hard to explain. Furthermore, Han et al. (2002) reported that unilateral presentation even decreased such a laterality effect. While our results are consistent with these data, the link with these studies remains somehow suggestive as the local and global terms in the latter studies refer to hierarchically related stimulus attributes in patterns like the ones introduced by Navon (1977), where attention is switched between the global and local stimulus levels and this phenomenon also does not explicitly deal with occlusion.

Amodal completion is akin to other filling-in processes, in which the percept exceeds the physical stimulus. These processes happen automatically, and furthermore we are generally not aware that we are making inferences that go beyond the information actually present in the stimulus. These filling-in processes include filling-in missing information from the blind spot and modal completion (i.e., the perception of illusory contours and surfaces; for an overview, see Pessoa et al., 1998). However, there is a difference in the phenomenological strength as we actually experience the filling-in from the blind spot and modal completion with a much stronger presence than is the case in the present amodal completion phenomena. In contrast to modal completions, amodal completions have no clear phenomenological presence. Investigating modal completions, several fMRI and MEG experiments found evidence for activation in the primary cortex, in the extrastriate cortex, and in the Lateral Occipital Region, the LOR (Hirsch et al., 1995; Kruggel et al., 2001; Meng et al., 2005; Seghier et al., 2000; Mendola et al., 1999; Ohtani et al., 2002; Halgren et al., 2003). For example, in a study comparing responses to modal completions and physical contours, Mendola et al. (1999) reported many similarities in activations and, recently, Meng et al. showed activations in early areas of the visual system (V1, V2) when perceiving certain kinds of modal completions (filling-in of luminance gratings, so-called visual phantoms, Meng et al., 2005). It is suggested that activation in the LOC region is related to segmentation of figures from the background, which also adds to the theoretical and psychophysical evidence for a surface-based representation of visual images (Kourtzi and Kanwisher, 2001; Nakayama and Shimojo, 1992). Our findings are consistent with these surface-based representations as we also show the importance of the overall surface in amodal completion. However, this does not imply that modal and amodal completions share the same underlying processes (Davis and Driver, 1997), although a recent study by Murray et al. (2004) showed an initial common mechanism for both (also including LOC) and a differential mechanism at a later stage.

Although amodal completion is phenomenologically not as strong as modal completion, we also find evidence for the actual formation of amodal completions. More importantly, these data go a step further in not only showing brain correlates of completions, but also providing more evidence for the influence of global context on amodal completion. This presence of global influences is reflected in an early and a late component. All in all, this is the first study to show brain responses relating to global and local context in amodal completion, and with that, the relevance of overall figural properties for amodal completion is supported.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2006.05.008.

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