The spatial gradient of visual masking by object substitution

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Abstract

A mask that has a common onset but delayed offset with the target produces substitution masking, which can be distinguished from pattern masking and metacontrast masking. This study tests the spatial properties of substitution masking: specificity to the target location and asymmetry to the central and the peripheral sides of the target. Results revealed that substitution declined gradually as the mask moved away from the target. Masking was stronger and its gradient declined more slowly as the eccentricity of the target increased. Substitution was asymmetric, stronger for peripheral than central masks. Results are consistent with a refined model of object substitution based on reentrant visual processing. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The seemingly effortless act of visual perception is a complex process involving activation of neurons at multiple stages of the nervous system (Felleman & van Essen, 1991). Visual input is received in the retina, passed on to the thalamus, and then to the visual cortex (Palmer, 1999). In parallel to this bottom-up projection, later visual areas also send feedback signals to earlier ones (Ito & Gilbert, 1999; Lamme, Super, & Spekreijse, 1998; Murphy, Duckett, & Sillito, 1999; Sillito, Jones, Gerstein, & West, 1994; van Essen & Maunsell, 1983). Although forward and backward projections typically initiate and end at different layers of the visual cortex (van Essen & Maunsell, 1983), both are directly involved in visual recognition. They form interactive loops that determine perceptual experience (Hupe et al., 1998).

It has now become well accepted that feedback connections can modulate bottom-up processing through attentional effects (Maunsell, 1995). For example, the receptive field of a neuron becomes more contracted when it falls inside rather than outside of the spotlight of attention (Luck, Chelazzi, Hillyard, & Desimone, 1997; Moran & Desimone, 1985; Motter, 1993; Treue & Maunsell, 1996). This has been shown in higher visual areas such as V4, IT, MT/MST (Maunsel, 1995; Treue & Maunsell, 1996), as well as lower visual areas such as V1 and V2 (Luck et al., 1997; Motter, 1993). Backward projections do not just modify visual recognition at terminal stages right before information reaches awareness; they directly and continuously affect visual processing at intermediate levels. Feedback processing joins forward processing early on, and they become integrated to provide input to the next stage of processing (Martinez et al., 1999).

Visual reentrance—the interactive loop of processing between forward and backward visual projections—is an important but elusive property of visual perception. Di Lollo, Enns, and colleagues recently discovered a behavioral effect that appears difficult to explain without the notion of visual reentrance (Bischof & Di Lollo, 1995; Di Lollo & Enns, 1998; Di Lollo, Enns, & Rensink, 2000; Enns & Di Lollo, 1997). In their object substitution masking tasks, Di Lollo and Enns (1998) presented observers with a search display containing

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geometric figures, one of which is the target, designated by a cue—four dots that form the corners of an imaginary square centered on the target. In the control condition, the search items along with the four-dot cue were presented simultaneously and immediately erased together (e.g. in 30 ms). Observers were typically good at identifying the shape of the target. In the condition of central interest, the items and the four-dot cue were presented together for a short period; then the search array disappeared, leaving the four-dot cue behind for a little longer (e.g. 160 ms). Performance in this *delayed offset* condition deteriorated dramatically compared with the control, *simultaneous offset* condition. The lingering four-dot cue functioned as a *mask*, disrupting the target's identity. Phenomenally, it appears as if the target was replaced by the surface of the imaginary square, showing masking by object substitution.

Substitution masking defies a satisfactory explanation based on existing theories of visual masking. First, the four-dot mask and the target have common onsets, and masking is robust no matter how long the mask persists, disobeying the onset-onset law of metacontrast masking (Kahneman, 1967) and ruling out explanations based on the transient properties of mask onset and offset (Breitmeyer, 1984; Breitmeyer & Ganz, 1976; Breitmeyer & Kersey, 1981). Second, the contours of the four-dot mask do not resemble that of the target. There is, in fact, very little contour in the mask. This rules out explanations based on low-level contour interaction between the target and the mask (Alpern, 1953; Breitmeyer, 1984). Finally, substitution masking does not result from the significantly longer mask duration than target duration (Weisstein, 1968), because masking is absent if the longer mask precedes rather than trails the target.

Di Lollo et al.'s (2000) model of object substitution proposed that the masking is a result of visual reentrance. According to this model, information is initially projected from lower to higher levels. The first wave of feed-forward processing, however, is typically not sufficient for perceptual identification, either because the input is consistent with more than one top–down hypothesis, or because the processing at later visual areas is too coarse for identification. As a result, identification is aided by feedback processing. The comparison between information at higher and lower areas allows a percept to be achieved, ensuring that the percept is consistent with processing at both the lower and the higher visual areas. In the *simultaneous offset* condition, nothing is left on the display once the target is erased. So later areas continue to process the trace of the target without being disrupted. In the *delayed offset* condition, the reentrant process retrieves the four-dot mask at the target location. The representation of a four-dot mask at earlier areas is inconsistent with the representation of a target shape at later areas, leading to confusion in processing and disruption of target identification.

Following this explanation, the object substitution paradigm can provide a window to study properties of visual reentrance. Applying this logic, we have recently examined what the reentrance mechanism treats as an inconsistency (Jiang & Chun, 2001). Our experiments revealed that a mask adjacent to the target could produce substitution, allowing us to test various kinds of masks that did not spatially overlap with the target. We varied the type of the mask and measured the extent of masking. Using letters as the elements on the search display, we found that substitution masking was not affected by (1) the categorical similarity between the target and the mask (letter vs. reflected letter, symbol vs. random dots) or (2) the feature similarity between the mask and the target (mask composed of lines and line junctions vs. mask composed of random dots). Substitution was reduced when the density in the mask was reduced, but only at the lower (sparse) extreme of mask density.

We believe that it is the spatio-temporal inconsistency between the target and the mask that matters, not shape or semantic inconsistency. Delayed offset of the mask renders it to be a different object than the target; the delayed offset alone is sufficient to trigger substitution in its full strength. Further inconsistency in the features or semantics of the visual items does not increase masking. Density of the mask matters because it affects the goodness of an object, particularly for displays with minimal features. Thus, it is the mask as a 'token' rather than a 'type' that leads to inconsistency in visual reentrance (for a discussion of types and tokens, see Chun, 1997; Kahneman, Treisman, & Gibbs, 1992; Kanwisher & Driver, 1992). Almost any stimulus type is sufficient to produce substitution masking.

In this study, we investigate the location specificity of substitution masking. Here we ask whether reentrance is restricted to the location of the target. On the one hand, substitution cannot be totally insensitive to target location. Because multiple objects typically co-occur, a reentrant process that is non-specific to location would compare information from different locations and lead to incorrect visual recognition. On the other hand, cells in later visual areas are associated with larger receptive field size (Desimone & Duncan, 1995), resulting in a loss of spatial resolution. These theoretical considerations lead to the prediction that substitution masking should be somewhat, but not completely, location specific.

To test the spatial specificity (spatial gradient) of visual reentrance, we systematically varied the distance between the target and the mask (Experiments 1 and 2) and the eccentricity of the target (Experiment 2). In fact, our previous study had obtained initial evidence

that substitution masking was not completely location specific (Jiang & Chun, 2001). That is, we found significant substitution when the mask was centered 1.1° away from the target positioned at an eccentricity of 3.13°. The current study extends this result by testing a larger range of target–mask distances and target eccentricities. Such psychophysical data are necessary to reveal how target and masks interact across the entire visual field, and hence they will provide informative constraints on models of substitution masking and reentrant processing.

2. Experiment 1: gradient of visual reentrance

In this experiment, observers were required to identify the sole black letter flanked by four white letters on each side. The display resembles the flanker paradigm introduced by C. W. Eriksen and colleagues (e.g. Eriksen & Eriksen, 1974). Four small dots were positioned to form an imaginary square, which served as the mask. The imaginary square was centered on one of the nine letters, randomly selected. Its distance from the center of the target letter thus varied at five levels: 0°, 0.94°, 1.88°, 2.81°, or 3.75°. The onset of the mask was simultaneous with the onset of the letter array, but its offset was either simultaneous with the offset of the letter array, or was delayed by 160 ms. The eight flanking letters served as distractors to increase the difficulty of target search, as larger set size is known to lead to larger substitution (Di Lollo et al., 2000). Fig. 1 shows a sample of the display used in this experiment. The difference in identification accuracy between the simultaneous and the delayed offset conditions is the measure of substitution masking. We are interested in how it is affected by the distance between the target and the mask.
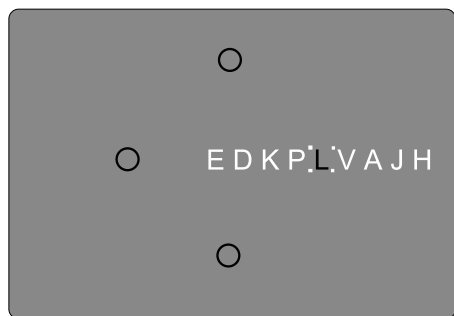

Fig. 1. A sample display used in Experiment 1. Letters were arranged in a linear array presented on the horizontal or vertical meridian in separate blocks. The four-dot mask could be centered on the target (as shown here) or on any of the flankers. When shown on the horizontal meridian, the target could be at the 3 or 9 o'clock positions; when shown on vertical meridian, the target could be at the 6 or 12 o'clock positions. These locations were illustrated by the black circles, which were not actually presented. Observers fixate at a central cross prior to the presentation of the target display.

Previous studies on pattern masking and on metacontrast masking indicated that visual lateral masking was reduced as the spacing between the target and the mask increased (Bouma, 1970; Breitmeyer, 1984; Wolford, 1975). For metacontrast masking, close spatial proximity is a necessity for the masking to occur. The effect of spatial separation interacts with target eccentricity. As the target moves away from the fovea, metacontrast masking increases and can be obtained at a farther target–mask separation (Breitmeyer, Rudd, & Dunn, 1981; Growney & Cox, 1977). Other types of lateral masking also work in close spatial proximity, decreasing as the distance between the target and the mask increases or as the target moves toward the fovea (Wolford, 1975).

Likewise, we expect substitution masking to decline as the distance between the target and the mask increases. However, this decrease cannot be accounted for by the same mechanism that contributes to metacontrast masking or lateral masking. First, the onset interval between the mask and the target is zero in substitution masking. At this interval, metacontrast masking is weak (Kahneman, 1967). Second, since general lateral masking (and hence the effect of crowding, e.g. Bouma, 1970; He, Cavanagh, & Intriligator, 1996) occurs equally in both the simultaneous and delayed offset conditions, the subtraction of the two conditions should remove the impact of lateral masking and crowding. The effect of spacing in lateral masking can be easily explained by low-level visual interactions such as feature perturbation (see Wolford, 1975). As we inferred earlier, the diminished spatial resolution at higher visual areas is the key to the distance effect in substitution masking. Because higher visual areas have poorer spatial resolution than lower areas, the visual reentrant process is bound to operate beyond the exact location of the target. What is not clear, however, is how substitution masking changes as the distance between the target and the mask increases. What is the shape and extent of this gradient, and at which distance does substitution masking interference disappear?

2.1. Method

Participants: Fourteen naïve college students from Yale University volunteered in the experiment. All reported normal color vision and normal or corrected-to-normal visual acuity. Their ages ranged from 18 to 28. Written consent was obtained before the experiment from each observer.

Stimuli and materials: Nine letters in a linear array were presented on the horizontal or the vertical meridian. The main task was to identify the single black letter in the array of white letters. When shown on the horizontal meridian, the target could be at the 3 or 9 o'clock positions; when shown on the vertical meridian,
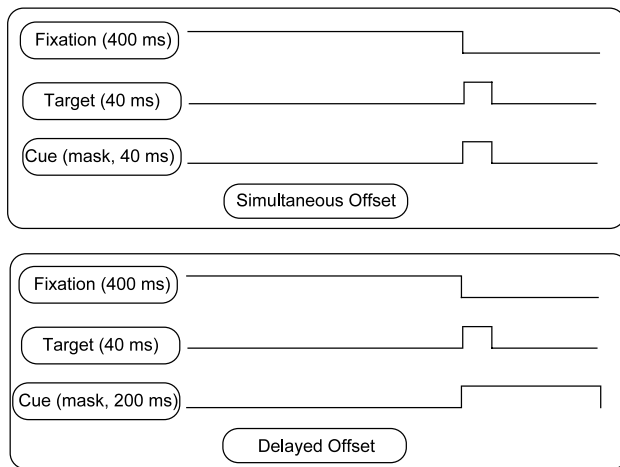
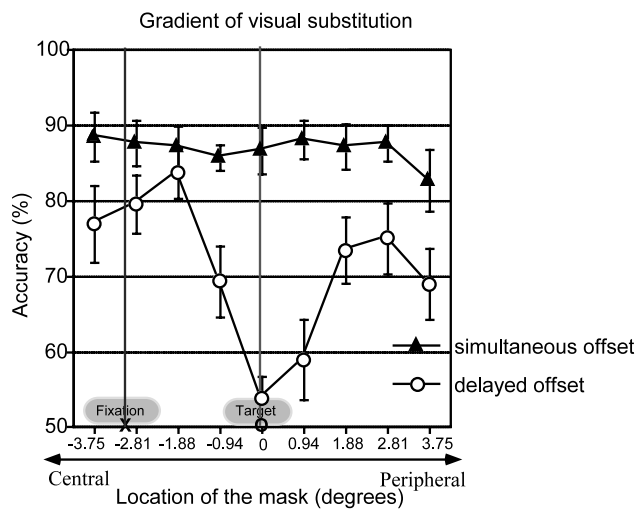Fig. 2. Presentation sequence used in Experiment 1.

Fig. 3. Results from Experiment 1. '**X**' and '**O**' shows the location of the fixation and that of the target, respectively. Standard error (subject variation) is shown on the error bars.

the target could be at the 6 or 12 o'clock positions. The letters were printed in Helvetica font with a point size of 32 ($0.7 \times 0.9°$). The center-to-center distance between adjacent letters was $0.94°$. The central letter was the target. It was the only black letter, flanked by four white distractors on each side. Its distance from the center of fixation was $3.13°$. The letters were randomly selected from upper-case alphabets (excluding 'I') with the constraint that the same letter could not repeat on a given trial. The background of the display was gray.

Each dot in the four-dot mask subtended $0.15 \times 0.15°$; the inner side of the imaginary square was $0.94°$. The four-dot mask was centered on the target, or on any of the flankers, equally often.

Trial sequence: Each trial started with a fixation (a cross subtending $0.3 \times 0.3°$) for 400 ms, followed by a search display of 40 ms. The letters were then erased, either along with the offset of the four-dot mask (simul-

taneous offset), or leaving the four-dot mask behind for 160 ms (delayed offset; see Fig. 2). Observers were prompted to enter the identity of the target on the keyboard, rewarded by three high-pitched tones after a correct response. They pressed the space bar to initiate the next trial.

Each observer received two experimental blocks, each with 144 trials ($144 = 2$ mask offset condition (delayed vs. simultaneous) $\times 9$ mask location $\times 8$ observations at each combination of mask offset and location). Each block was preceded by 72 trials of practice. One of the blocks presented stimuli on the horizontal meridian, the other on the vertical meridian. The order of the orientations was counterbalanced across observers. Analyses were performed by combining the two blocks, because unpublished data from our lab showed similar pattern of substitution on the horizontal and the vertical meridians.

Equipment: The experiment was conducted on a Macintosh computer (PowerPC) with a 17″ monitor. The task was programmed with MacProbe software (Hunt, 1994). Observers were tested individually in a room with normal interior lighting. They sat at a distance of 57 cm from the computer screen with a chinrest to maintain constant viewing distance.

2.2. Results

Fig. 3 shows mean accuracy as a function of mask offset and mask location.

Note that the four-dot mask could be on the central side of the target (closer to the fixation than the target is) or the peripheral side. Although the absolute distance between the target and the four-dot mask was identical for central and peripheral masks, we previously reported an asymmetry of larger masking from peripheral masks (Jiang & Chun, 2001). So we treated these locations as different levels of the distance factor in the first ANOVA test.

2.2.1. Overall analysis

An ANOVA test with mask offset (delayed vs. simultaneous) and mask location (one of the nine locations) revealed significant main effects of mask offset, $F(1, 13) = 49.48$, $P < 0.0001$, with poorer performance in the delayed offset condition; and mask location, $F(8, 104) = 8.65$, $P < 0.0001$, with poorer performance as the mask was closer to the target. There was also a significant interaction between mask offset and location, implying a gradient of substitution surrounding the target, $F(8, 104) = 7.62$, $P < 0.0001$, with stronger substitution nearer the target.

The largest substitution appears to occur when the mask and the target were centered at the same position. Comparing the conditions when the mask was centered on the target and on the adjacent, *central* flanker (the

'−0.94' location on Fig. 3), there were significant effects of mask offset, mask location, and their interaction (all $Ps < 0.028$). As the mask moved from the target location to the adjacent, *peripheral* flanker (the '0.94' location on Fig. 3), however, the reduction in substitution masking was not statistically significant, $F < 1$. As the mask moved from the target location to two steps away toward the peripheral direction (the '1.84' location on Fig. 3), substitution was significantly reduced ($F(1, 13) = 17.65$, $P < 0.001$). Thus, with the exception of the adjacent, *peripheral* flanker, substitution appears to be strongest when the mask was centered on the target, showing location specificity in visual reentrance.

Nevertheless, substitution was not eliminated when the target and the mask were at different locations. Pair-wise comparisons revealed significant substitution masking for a mask centered on a central flanker 0.94° away from the target ($P < 0.004$) and 3.75° away ($P < 0.014$); and significant masking for a mask centered on a peripheral flanker 0.94° away from the target ($P < 0.0001$), 1.88° away ($P < 0.001$), 2.81° away ($P < 0.009$), and 3.75° away ($P < 0.001$). Visual inspection revealed a gradient of substitution at these locations, and an asymmetry in substitution.

2.2.2. When the mask was centered on the flankers

We then restricted the analysis to the conditions when the mask was away from the target. An ANOVA on mask side (central vs. peripheral), mask location (0.94°, 1.88°, 2.81°, or 3.75° away from the target), and mask offset (delayed vs. simultaneous) revealed significant main effects of mask offset, $F(1, 13) = 31.29$, $P < 0.0001$, showing substitution masking; mask side, $F(1, 13) = 14.42$, $P < 0.002$, showing poorer performance for peripheral masks; and mask location, $F(3, 39) = 6.60$, $P < 0.001$, showing better accuracy as the mask moved further away from the target.

Importantly, there was a significant interaction between mask offset and mask location, $F(3, 39) = 6.86$, $P < 0.001$, showing reduced substitution masking as the mask was further away from the target. The interaction between mask offset and mask side was significant, $F(1, 13) = 14.10$, $P < 0.002$, indicating asymmetric substitution. Using fixation as the reference point, substitution was stronger when the mask was toward the peripheral (far) side of the target rather than the central (near) side. This replicated our earlier finding (Jiang & Chun, 2001). The interaction between mask side and mask location was not significant, $F < 1$, nor was the three-way interaction, $F = 1$.

Follow-up tests showed that when the mask was one-step away from the target (0.94°), substitution masking was significant ($P < 0.0001$), as well as the asymmetric pattern (i.e. the interaction between mask offset and mask side; $P < 0.009$). Both substitution masking and asymmetric substitution were also significant when the

mask was two-steps away (1.88°), $Ps < 0.022$. As the mask moved to three-steps away (2.81°), substitution masking was significant ($P < 0.011$) but the asymmetric masking pattern was not, $F < 1$. At four-steps away (3.75°), substitution was significant ($P < 0.0001$); overall accuracy was poorer for peripheral masks ($P < 0.001$); but substitution masking was of the same magnitude for central and peripheral masks, $F < 1$. It appears that asymmetric substitution was more apparent when the mask was closer to the target (i.e. within 2°). Nevertheless, the three-way interaction between mask side, mask location, and mask offset was far from significant ($F = 1$), arguing against the idea that asymmetric substitution was qualitatively different at varying distances.

2.3. Discussion

Three noteworthy results were obtained from Experiment 1. First, there appeared to be a gradient of substitution masking surrounding the target, with strongest substitution when the mask was centered on the target, and reduced masking as the mask moved away from the target. Second, the gradient of substitution was asymmetric to the central and the peripheral side of the target. Substitution was stronger when the mask was toward the peripheral side of the target, using fixation as the reference point. The asymmetry was most apparent when the mask was within 2° of the target, although it may not be completely eliminated at farther distances. Third, although significantly reduced, substitution masking did not disappear at a separation between the target and the mask of 3.75°, the largest distance tested in this experiment.

The gradient of substitution masking is consistent with the idea that visual reentrance is location specific, but the spatial resolution of neurons in later visual areas is not accurate enough to prevent reentrant processing from spreading to areas surrounding the target. At a target eccentricity of 3.13°, substitution masking was robust even when the distance between the target and the mask was 3.75°, a value that seems quite large to us. This suggests that the spatial resolution of some of the neurons involved in visual reentrance is poorer than 3.75°.

3. Experiment 2: parametric testing of substitution masking

The receptive field size of cells changes not only across visual levels, but also within the same level. In the latter case, the receptive field size increases as the eccentricity increases. In this experiment we tested how the gradient of substitution masking is affected by the visual eccentricity of the target. We predict that across a range of visual eccentricity, substitution should reduce as the spatial

separation between the target and the mask increases, but the gradient of substitution should spread to larger target–mask distances as the eccentricity increases. There were several changes made to the presentation.

First, rather than presenting the target at a fixed eccentricity, in Experiment 2 target eccentricity varied at three levels: 3°, 6°, and 9°. Target eccentricity should produce two effects on substitution masking. First, because shape processing in peripheral vision is slower and less accurate, the chance of visual reentrance increases as the eccentricity of the target increases. Substitution masking should be larger if the target is more eccentric. Di Lollo et al. (2000) showed exactly this result when the target and the mask were centered at the same position and target eccentricity was varied. Second, neurophysiological studies have shown that the receptive field size of cells gets larger as the receptive field moves from fovea to periphery (e.g. Piñon, Gattass, & Sousa, 1998). This in turn leads to poorer spatial resolution for cells whose receptive fields are at larger eccentricities (Carrasco, McLean, Katz, & Frieder, 1998; Robson & Graham, 1981), resulting in reduced location-specificity in visual reentrance. For a more eccentric target, substitution masking should persist across larger target–distractor distances.

Second, the center-to-center distance between the target and the mask varied at five levels: 1.5°, 2.0°, 4.0°, 8.0, and 10.0°. These values covered a larger range of distances than Experiment 1 and increased the chance for substitution masking to disappear. If the gradient of substitution masking was due to reduced spatial resolution in visual reentrance, we should find diminished substitution when the target–mask distance becomes so separated that it can be resolved by all cells involved in visual reentrance.

Third, to reduce extraneous noise we omitted the presentation of distractors. This unavoidably resulted in smaller substitution masking, as smaller set size was associated with less reentrance (Di Lollo et al., 2000). To boost the power of detecting substitution masking, we used a denser mask than the four-dot mask of Experiment 1. The dense mask was composed of 50 pixels randomly filling in a 10 × 10 invisible matrix that subtended 1 × 1°. In contrast, the four-dot mask used in Experiment 1 contained 36 pixels in total. Because the mask was no longer a hollow square, centering the mask and the target at the same position would lead to contour overlap between the two. Thus, the mask was always centered at a different location than the target in this experiment. Observers' task was to identify the single white letter.

3.1. Method

Participants: One author (Y.J., female, 25, practiced)

and two naïve observers (A.W., female, 27; and X.L., male, 29) volunteered in the experiment. All had normal color vision and normal or corrected-to-normal visual acuity. Written consent form was obtained before the experiment.

Stimuli and materials: Each observer sat at a distance of 29 cm away from the computer screen with a chinrest to maintain constant viewing distance. The target was a white letter (0.8 × 1.0°) randomly selected from upper case alphabets (excluding 'I'). The mask was created by using white pixels to fill in 50 cells randomly chosen from an invisible matrix (10 × 10 matrix subtended 1.0 × 1.0°). The background of the screen was gray.

The target and the mask were always presented on the horizontal meridian. The target was centered at an eccentricity of 3°, 6°, or 9° to the left or right of fixation. The center-to-center distance between the target and the mask was 1.5°, 2°, 4°, 8°, or 10°. The mask could be on the peripheral or the central side of the target.

Procedure: Each trial started with a fixation (a cross subtending 0.3 × 0.3°) at the center of the display for 400 ms, followed by a search display of 27 ms. The letter was then erased. The mask either disappeared along with the target or stayed for 160 ms longer. Observers typed in the target letter on the keyboard, with a tone rewarding correct responses.

There were three testing sessions, each involving 10 blocks. Each block contained 120 trials (120 = 2 (mask offset time) × 3 (target eccentricity) × 2 (target to the left or right of fixation) × 5 (target–mask distance) × 2 (mask side)). Observers also received a practice block of 16 trials preceding each testing session.
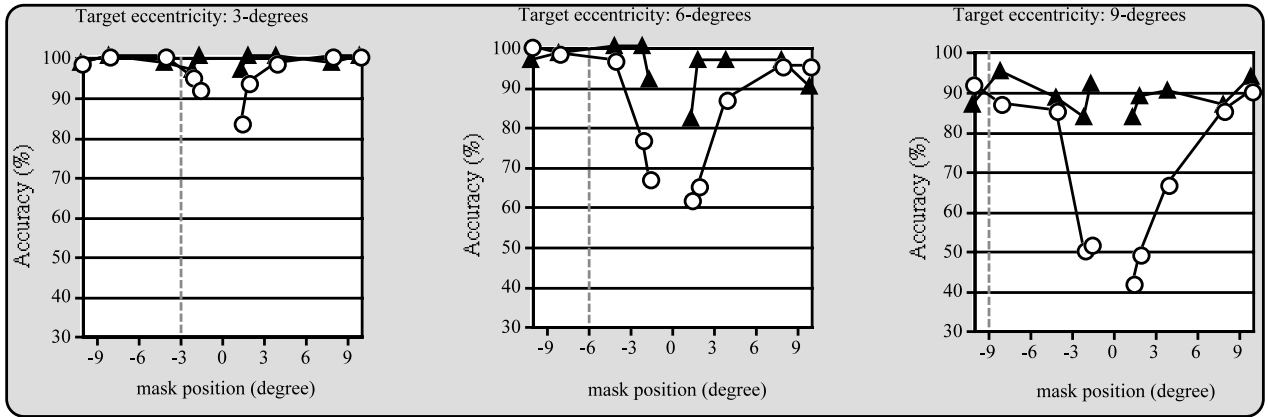
3.2. Results

Fig. 4 shows the results from individual observers. To obtain an index of the magnitude of substitution masking, we calculated the area of the delayed offset curve below the simultaneous offset curve. Fig. 5 shows this index as a function of target eccentricity.

The observers were consistent in the following effects. First, the more eccentric the target was located, the larger the substitution masking. This held up for central as well as peripheral masking. Second, the closer the mask was to the target, the larger the substitution.[1]

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[1] We note that the use of a denser mask positioned at a different location from the single item (i.e. the target) produced a percept of apparent motion between the target and the mask, particularly at the closer target–mask seperations (e.g. 1.5° and 2°). Apparent motion is known to suppress target identification (Bischof & Di Lollo, 1995), and it could be perceived in our delayed offset but not the simultaneous offset condition. In turn, the masking measured is a summed effect of suppression and delayed offset masking. It is also possible to view the suppression effect of apparent motion as a form of object substituition.
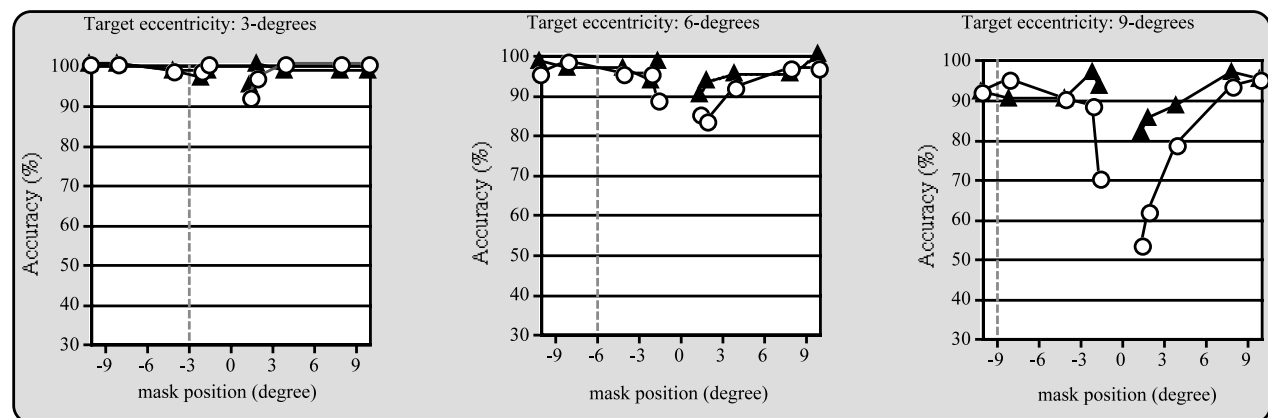
Subject A.W., Female, 27

Subject X. L., Male, 29
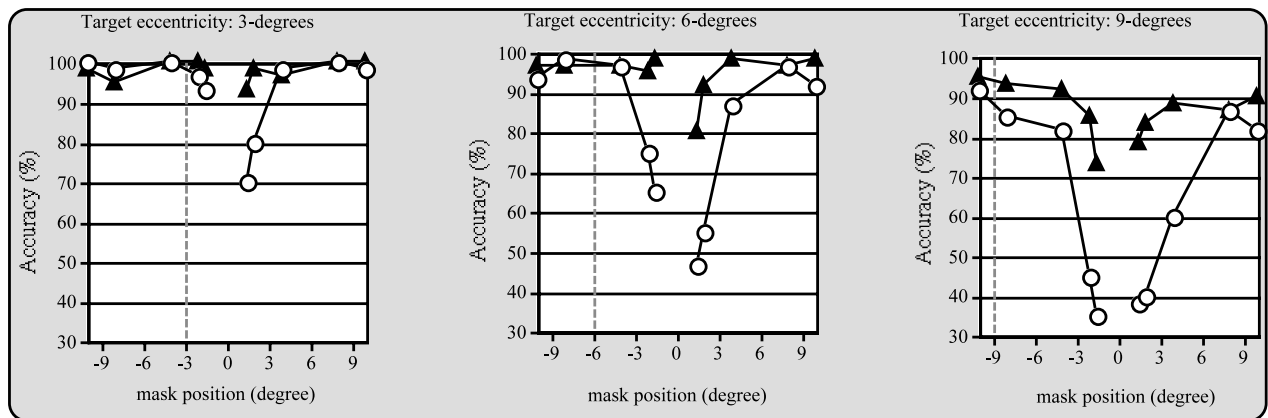
Subject Y.J., Female, 25

—○— delayed offset

—▲— simultaneous offset

Position of the fixation point

Fig. 4. Results from Experiment 2. Observer Y.J. is practiced; A.W. and X.L. are naïve.

Substitution gradually disappeared as the distance separating the target and the mask got longer. The distance at which substitution masking was eliminated (became zero) depended on the eccentricity of the target and the spatial arrangement of the target and the mask. As target eccentricity increased, the spatial range of substitution masking increased. Holding the eccentricity of the target constant, a larger separation was needed for
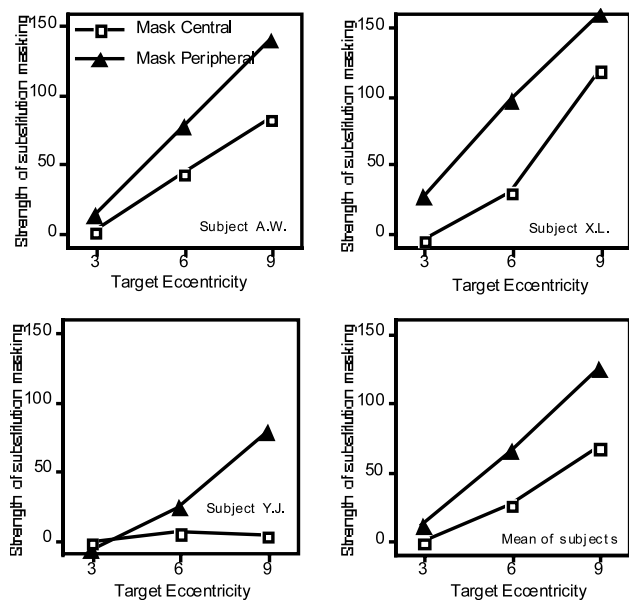
Fig. 5. Magnitude of substitution masking: area of the delayed offset curve underneath the simultaneous offset curve in Experiment 2. The *Y*-axis is the area of curve underneath the simultaneous and the delayed offset conditions shown in Fig. 4.

masking to disappear for peripheral than central masks. Table 1 shows an estimate of the distance between the target and the mask at which substitution masking disappeared. Third, substitution was stronger for peripheral than central masking and decayed more slowly with target–mask distance.

3.3. Discussion

The results from Experiment 2 can be nicely explained by the assumption that visual reentrance is somewhat, but not perfectly, specific to the target location. Properties of receptive field size at various levels of visual processing can account for the effects of eccentricity and distance. At larger eccentricities cells have larger receptive field size. This leads to reduced spatial resolution, which in turn increases processing time. These properties are nicely reflected by increased substitution masking and reduced spatial specificity at more eccentric locations of the target.

Properties of receptive field size account for eccentricity effects, but not the asymmetry in substitution. In Experiments 1 and 2, substitution masking was larger and disappeared more slowly when the mask fell to the peripheral side rather than the central side of the target. We have previously explored the basis of asymmetric substitution and have ruled out a few explanations of this phenomenon (Jiang & Chun, 2001). In particular, we ruled out an explanation that focuses on the differences in eccentricity between the central and the peripheral masks. There are two variations of this account. First, because the receptive fields of cells tend to be larger at more eccentric locations, a peripheral mask falls on cells with poorer spatial resolution. The gradient of substitution therefore drops more slowly for peripheral masks than central masks. Second, visual acuity is reduced as the eccentricity of the target increases. In addition, the functional eccentricity of the target is determined not by the center of the target, but by the center of the perceptual group encompassing the target and the mask (Banks, Larson, & Prinzmetal, 1979). A peripheral mask increases the eccentricity of the target–mask group, resulting in impaired visual acuity.

Although eccentricity factors may exaggerate asymmetric substitution, direct tests showed that it was not critical. In one experiment, we presented the mask at a fixed eccentricity, and the target at a more central or more peripheral location than the mask (Jiang & Chun, 2001). In this case, a central target should benefit from high spatial resolution and high visual acuity. Yet substitution masking was stronger for a central target than a peripheral target. Thus, when the mask is relatively more peripheral than the target, it produces larger substitution, even though the target itself is closer to the fixation. A relatively more peripheral mask (compared to the target) leads to stronger substitution, overriding the effect of target eccentricity.

To account for asymmetric substitution, we hypothesized that in addition to visual reentrance, later visual areas send inhibitory projections down to earlier areas to reduce interference from surrounding distractors and the mask. The inhibition is centered on the target and is hypothesized to be stronger toward the central side of the target. As a result, a mask presented to the central

Table 1
Estimated separation between the target and the mask at which substitution masking disappeared

| Mask side | Target = 3° | | Target = 6° | | Target = 9° | |
	Central	*Peripheral*	*Central*	*Peripheral*	*Central*	*Peripheral*
A.W.	1.5–2°	2–4°	2–4°	4–8°	8–10°	8–10°
X.L.	1.5–2°	2–4°	4–8°	4–8°	8–10°	8–10°
Y.J. (practiced)	0–1.5°	0–2°	1.5–2°	4°	2–4°	8–10°

side of the target is inhibited more strongly and less substitution is observed. Converging evidence for the inhibition account came from a visual search task in which the mask was not presented (Jiang & Chun, 2001). Observers searched for a uniquely colored letter among competing distractors. On 25% of the trials a small dim dot was presented either to the central or the peripheral side of the target. Probe detection was significantly slower and less accurate when the probe was to the central side of the target, confirming stronger inhibition at that position. Importantly, probe detection was equally good at both sides of the target once the distractors were removed, adding credibility to the idea that the asymmetry is a result of inhibition, triggered by the presence of distractors (Jiang & Chun, 2001). The asymmetric inhibition account is not completely ad-hoc, given that a central mask competes more strongly with target processing and may require more inhibition to dampen its interfering effect.

4. General discussion

In two experiments, we tested the spatial properties of visual reentrance using the substitution paradigm. Experiment 1 presented the mask at varying distances away from the target at a fixed eccentricity of 3.13°. Results showed a gradient of substitution surrounding the target, with stronger masking when the mask was closer to the target. Masking was not completely eliminated even when the mask was 3.75° away from the target, the maximal distance tested in Experiment 1. This indicates that visual reentrance is somewhat location specific, but the accuracy of location representation is far from perfect. Experiment 2 varied target eccentricity and the distance between the target and the mask. For a more eccentric target, substitution was stronger and disappeared at farther target–mask distances. In addition, visual reentrance was stronger when the mask fell to the peripheral rather than the central side of the target.

These results fit in with Di Lollo et al.'s (2000) model of object substitution. Simply speaking, the recognition of a visual object is jointly determined by bottom–up input and feedback reentrance. The longer the target processing takes, the more opportunity there is for reentrance to pick up a conflict of visual information between different areas. Substitution masking is thus affected by the difficulty of target processing, as well as visual attention. The model is not restricted to the common onset masking paradigm; it applies to typical metacontrast masking (Di Lollo et al., 2000), which may be sensitive to high-level factors such as attention (Ramachandran & Cobb, 1995) and objecthood (e.g. Williams & Weisstein, 1984).

This model can be extended with two additional assumptions. First, visual reentrance is specific to the location of the target, but the specificity is not perfect. It is limited by the spatial resolution of cells at a higher visual area sending reentrant feedback to lower visual areas. Our data are consistent with two general principles of receptive field size properties in the primate visual system (Desimone & Duncan, 1995). First, the receptive field size increases from earlier to later visual areas. When stimulation falls in the foveal region, the receptive field size is about 0.1–0.5° in area V1, 0.5–1.0° in area V2, 1–4° in area V4, and 25° or more in area IT (Desimone, Moran, & Spitzer, 1988). Second, within a particular anatomical area, the receptive field size increases at larger eccentricity. For example, in area V4 of the Cebus Monkey, the receptive field size (RFS) of a neuron can be roughly characterized as a linear function of eccentricity: $RFS = [0.4 + (0.31 \times \text{eccentricity})]$ (Piñon et al., 1998). These findings predict that substitution masking is not location-specific, forming a spatial gradient of decreased masking as mask distance increases away from the target. In addition, a larger range of interference is expected as target eccentricity increases.[2] All of these patterns were confirmed in our experiments.

Second, as suggested by our previous study, spatio-temporal inconsistency is sufficient for substitution masking. As long as display parameters present the target and the mask as different objects, as in the delayed offset condition, substitution masking will be triggered. Further inconsistency in the identity of the target and the mask does not increase masking (Jiang & Chun, 2001).

Although an extension of Di Lollo et al.'s (2000) object substitution model can readily accommodate our spatial gradient data, the reentrant model cannot naturally explain asymmetric substitution: larger substitution for a peripheral than a central mask. It appears that in addition to visual reentrance, later visual areas also send inhibitory connections to earlier areas in presence of distractor interference. The inhibition surrounds the target, and is stronger toward the central (near) side. This side is closer to fixation and thus a mask there may compete more potently with the target and therefore needs to be inhibited more strongly (Jiang & Chun, 2001).

Finally, on a speculative note, our data may point to one rough method for estimating the source of visual reentrance. As we have hypothesized, the existence of

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[2] Although we discuss the 'visual' receptive field size of neurons, we must note that top–down attention influences the effective receptive field size of neurons. The receptive field contracts when falling inside rather than outside of the attentional spotlight (Moran & Desimone, 1985). The gradient of attention is likely to play an important role in affecting RFS of neurons, which in turn determines the gradient of substituition masking observed in this study.

substitution masking for target and mask positioned at different locations is the result of coarse spatial resolution at higher visual areas. Specifically, if the spatial resolution of a particular visual region is worse than, say, 2°, then a mask positioned within 2° of the target will interfere with reentrant processing, producing substitution masking. Thus, the spatial separation at which substitution masking disappears is an estimate of the spatial resolution of the higher visual area involved in reentrant processing. Hypothetically, if one knows the size of the receptive field of cells at each visual areas, and how the size changes as a function of visual eccentricity; and if one maps out the distance at which substitution masking disappears, one may be able to infer the source of reentrant feedback processing. Currently, our data cannot pinpoint the physiological locus of visual reentrance, because one has yet to map out the receptive field of cells under comparable viewing conditions. Additional studies, conjoined with neurophysiological recordings, may provide additional clues to the source of visual reentrant processing.

Acknowledgements

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