Psychological Science

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Psychological Science 2010 21: 224 originally published online 19 January 2010
DOI: 10.1177/0956797609360664

Research Article

Psychological Science
21(2) 224–233

DOI: 10.1177/0956797609360664
http://pss.sagepub.com

Unconscious Numerical Priming Despite Interocular Suppression

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Abstract

Whether high-level properties of stimuli rendered invisible by interocular competition can influence perception and behavior remains controversial. We studied whether suppressed and invisible symbolic and nonsymbolic numerical stimuli can elicit priming. First, we established that participants were objectively unable to discriminate numerical prime stimuli when interocular suppression rendered them invisible. Next, we asked participants to enumerate a visible target set of items after being exposed to a suppressed, invisible (nonsymbolic or symbolic) prime set. Both symbolic and nonsymbolic unconsciously perceived numerical primes induced robust priming effects that were specific to the numerical distance between the target and prime. Comparison with a no-prime condition revealed that primes larger than targets interfered with target enumeration and primes the same as or smaller than targets facilitated target enumeration. Taken together, our findings provide clear evidence for high-level processing of stimuli rendered invisible through interocular suppression.

Keywords

consciousness, number comprehension, priming, mathematical ability

Received 6/13/08; Revision accepted 5/6/09

Identifying the processes for which awareness is necessary is a fundamental issue in the search for neural correlates of consciousness (Crick & Koch, 1995). Previous research suggests that extraction of higher-level categorical and semantic information during binocular rivalry may be such a process (Cave, Blake, & McNamara, 1998; Zimba & Blake, 1983). Line drawings of common objects presented to the suppressed eye during rivalry are not recalled subsequently and do not elicit repetition priming in a picture-naming task (Cave et al., 1998). Moreover, binocularly suppressed words do not prime same-category words in a lexical decision task (Zimba & Blake, 1983). These findings have led to proposals that visual information necessary for higher-level priming is lost through binocular suppression (Blake & Logothetis, 2002). However, the human dorsal stream can show category-specific responses to certain types of visual stimuli under conditions of profound interocular suppression (Fang & He, 2005), which suggests that at least some residual visual information from invisible stimuli can be processed in the dorsal stream. Whether this information includes semantic information or can result in behavioral effects such as priming remains unclear.

Several studies have implicated the human intraparietal sulcus (IPS) in the processing of symbolic numerosity (i.e., Arabic digits or number words; Dehaene, Piazza, Pinel, & Cohen, 2003) and nonsymbolic numerosity (e.g., patterns of rectangles or dots; Castelli, Glaser, & Butterworth, 2006; Piazza, Giacomini, Le Bihan, & Dehaene, 2003; Piazza, Mechelli, Butterworth, & Price, 2002). The IPS has also been implicated in visuospatial tasks, such as reaching (Hubbard, Piazza, Pinel, & Dehaene, 2005), that are the hallmark of dorsal-system function (Goodale & Milner, 1992). Given the evidence for this functional overlap in IPS, together with the evidence for parietal responses to invisible stimuli (Fang & He, 2005), we conjectured that numerosity judgments might exhibit subliminal priming during interocular suppression.

Unconscious processing for symbolic numerosity has been demonstrated in healthy humans (Naccache & Dehaene, 2001) and in neglect patients (Cappelletti & Cipolotti, 2006; Sackur et al., 2008). However, evidence for unconscious processing of nonsymbolic numerosities is sparse. Masked and invisible Arabic numerals can lead to facilitation of performance on

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a number-comparison task (i.e., smaller or greater than 5) involving Arabic numerals or dot patterns. However, invisible dot patterns prime only Arabic numerals, and not dot patterns, on the same task (Koechlin, Naccache, Block, & Dehaene, 1999), which suggests that enumeration of nonsymbolic items may not have access to unconscious information. In contrast, neglect patients can extract nonsymbolic numerosity information (up to 4) in a direct numerosity judgment for items in their neglected hemifield, despite being unaware of the identity and location of the items, a result suggesting that unconscious numerosity information (from the neglected hemifield) can indeed contribute to conscious enumeration (Vuilleumier & Rafal, 2000). It is thus conceivable that unconscious numerosity extraction is more amenable to investigation if small numbers are used (i.e., numbers smaller than 4), and that direct numerosity estimation (Vuilleumier & Rafal, 2000) is a more suitable task than numerosity comparison (Koechlin et al., 1999). Furthermore, the discrepancy between these findings is important because it is relevant to two general questions in numerical cognition: whether symbolic and nonsymbolic numerosities share a common representation (see Ansari, 2007, for a brief review), and whether adjacent numbers are represented as overlapping activations on a mental number line (Roggeman, Verguts, & Fias, 2007; Verguts & Fias, 2004) or represented accumulatively (Zorzi, Stoianov, & Umilta, 2005).

We therefore set out to answer two key questions. First, we sought to determine whether visual stimuli rendered invisible by interocular suppression can cause unconscious numerical priming. Such evidence would call into question the notion that unconscious processing during interocular suppression is restricted to low-level visual attributes (Blake & Logothetis, 2002). Second, we investigated whether nonsymbolic and symbolic invisible stimuli can cause unconscious priming, thus providing a parallel (in healthy, normal participants) to earlier neuropsychological studies of unconscious nonsymbolic numerosity processing in neglect patients (Vuilleumier & Rafal, 2000).

Method

Participants

A total of 73 healthy participants (46 females, 27 males; mean age = 21 years, range: 19–41) gave written informed consent to take part in five experiments (15, 21, and 18 participated in Experiments 1–3, respectively, and 19 participated in both Experiments 4 and 5). All had normal or corrected-to-normal vision and were naive to the purpose of the experiment. Participants received monetary compensation, and the experiments were approved by the local ethics committee.

Stimuli

Participants initiated each trial after achieving satisfactory binocular fusion of images viewed through a mirror stereoscope (see the Supplemental Material available on-line for the display parameters). Arrays of randomly generated shapes of rapidly changing (30 Hz) colors and forms, circumscribed by an outer square border (width = 5°), were presented to one randomly chosen, "dominant" eye. Meanwhile, a prime set consisting of a low-contrast numerical stimulus array was presented to the other, "suppressed" eye (see the next paragraph). This stimulus configuration (see Fig. 1), known as continuous flash suppression (CFS; Bahrami, Carmel, Walsh, Rees, & Lavie, 2008a, 2008b; Bahrami, Lavie, & Rees, 2007; Fang & He, 2005; Tsuchiya & Koch, 2005), reliably suppressed the prime from awareness in the majority of the trials (see Results). In Experiments 1 through 3, the prime duration was drawn from a uniform random distribution (range: 1,000–3,000 ms), whereas in Experiments 4 and 5, it was fixed to 1,000 ms. Binocular presentation of the mask array (duration varying from 500 to 1,000 ms) followed immediately, to overwrite the retinal afterimages induced by the prime set (Tsuchiya & Koch, 2005).

In Experiments 1, 2, 4, and 5, the prime set consisted of one, two, or three identically oriented Gabor patches (spatial frequency = 3.6 cpd) displayed against a gray background. In Experiments 1 and 2, contrast was randomly chosen from four steps in the range from 10 to 50%; in Experiments 4 and 5, contrast was fixed at 10%. Use of Gabor patches ensured that luminance was not confounded with number, and the size of the Gabors was randomized to avoid any correlation between surface area and number (see the Supplemental Material). The orientation of the Gabors was kept constant within each trial to avoid any correlation between variability and number, but was randomized across trials (uniform distribution; range: 1–180°). Location was randomly chosen for each Gabor with the constraint that no Gabor was placed closer than 0.5° from either the borders of the array or another Gabor. In Experiment 3, the prime set consisted of an Arabic digit (1, 2, or 3); location, contrast, and size were randomized as for the Gabor patches employed in Experiments 1 and 2.

In Experiments 2 through 5, a binocular target set was presented after the prime set (i.e., during the binocular presentation of the mask array; see Fig. 1). Target sets consisted of one, two, or three high-contrast (90%) Gabor patches, which, on top of the mask, looked like striped squares. The target set was always displayed for 200 ms, but its onset was slightly jittered (range: 100–200 ms) from the onset of the binocular mask. The orientation of the target set was randomly chosen for each trial (uniform distribution; range: 1–180°). All responses were made by manual press of a key on a computer keyboard.

Experiment 1

Experiment 1 investigated whether forced-choice report could access unconscious numerosity information. Each trial therefore ended with binocular presentation of the CFS mask without a target set. Participants were asked to first enumerate the

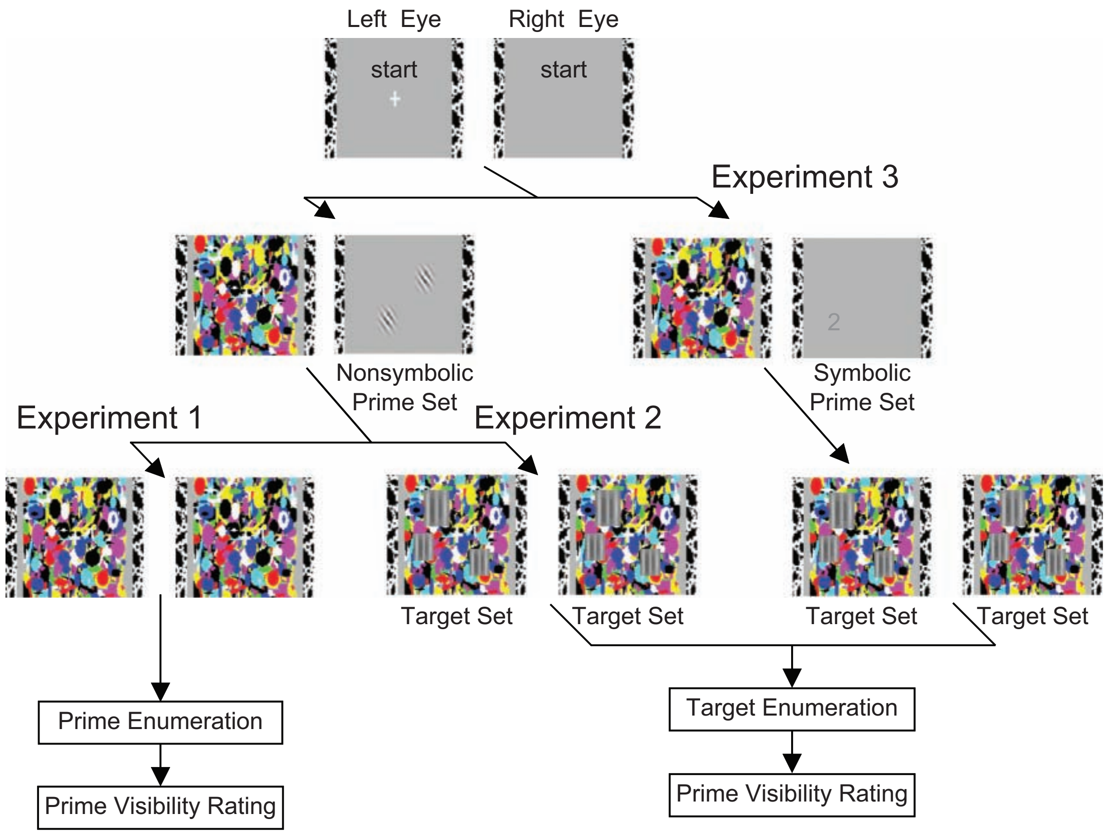

Fig. 1. Experimental design. The schematic shows the timeline and examples of stimuli for individual trials in the experiments. Initially, a blank gray stimulus was presented via a mirror stereoscope to each eye; the stimulus included flanking textured lines to aid binocular fusion. Subsequently, a symbolic or nonsymbolic numerical prime was presented to one eye (the suppressed eye) while a brightly colored texture background was shown to the other (the dominant eye). Some experiments also included a no-prime condition, in which only the gray background was presented to the suppressed eye. Finally, identical mask arrays consisting of the colored texture background were shown to both eyes. In Experiments 2 and 3, one, two, or three target stimuli were superimposed on this background; in Experiment 1, only the mask arrays were presented. Depending on the experiment, participants enumerated either the suppressed prime or the target stimuli (see the Method section for details) and then rated the visibility of the prime. Experiment 4 had the same design as Experiment 2 except that on some trials the prime set was presented binocularly in identical retinal locations and thus was visible. Experiment 5 was also similar to Experiment 2 except that participants were asked to enumerate the prime set and rate its visibility.

prime set (3-alternative forced choice) and then rate the visibility of the prime set (0 = *invisible*, 1 = *doubtful*, 2 = *clearly visible*). Accuracy, but not speed, was emphasized. Each participant completed five blocks of 48 trials after completing one practice block. Trials were binned according to visibility rating, and enumeration accuracy was calculated for each bin. Binomial tests were used to assess within-subjects statistical significance of enumeration accuracy (see the Supplemental Material).

Experiments 2 and 3

In Experiments 2 and 3, we investigated whether the unconscious prime set would induce priming effects on enumeration of the target set. Participants enumerated the target set as quickly as they could and then rated the visibility of the prime set. Clear differences in the characteristics of the prime set (Experiment 2: low-contrast striped circles; Experiment 3: one Arabic numeral) and the target set (high-contrast striped squares) ensured that participants had little difficulty reporting their subjective impression of the prime set's visibility. In these experiments, we also included a no-prime condition, in which only the gray background was presented to the suppressed eye during CFS. Thus, in these trials, the target was not preceded by a prime. Each participant completed one practice block and 10 to 12 experimental blocks of 36 trials.

Experiments 4 and 5

In Experiments 4 and 5, we sought to replicate the findings from Experiments 1 and 2 within a single group of participants, to compare the effects of conscious (binocular) and unconscious (monocular) priming, and to enhance the depth of suppression by reducing prime contrast and duration (for details, see the Supplemental Material). Experiment 4 was identical to Experiment 2 except for (a) the differences in the priming stimuli already noted and (b) the inclusion of a subset of trials in which the prime set was presented binocularly in identical retinal locations and thus was visible. Experiment 5 was identical to Experiment 4 except that participants were asked to enumerate the prime set and rate its visibility, and the no-prime condition was not included.

Results

Experiment 1

A forced-choice paradigm tested whether participants could explicitly enumerate small (< 4) numerosities in the prime set when they rated the set as invisible (i.e., a rating of 0). On average, visibility was rated 0 in 47% of trials, 1 in 27% of trials, and 2 in 26% of trials. Figure 2a shows the mean accuracy of numerosity judgment across participants ($N = 15$) as a function of visibility rating. Enumeration accuracy increased with visibility rating; a one-way analysis of variance (ANOVA)

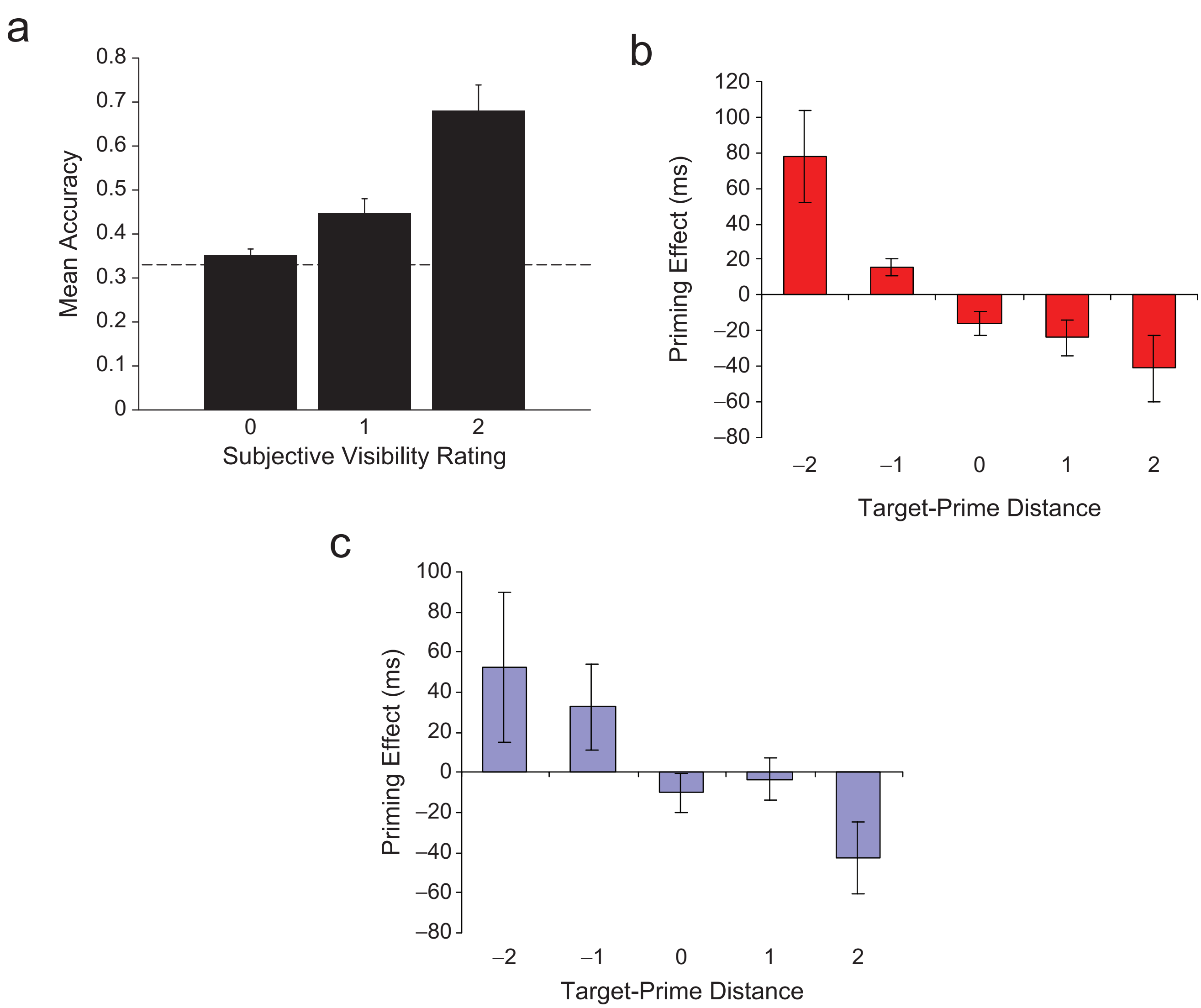

Fig. 2. Results from Experiments 1, 2, and 3. For Experiment 1 (a), mean enumeration accuracy (±1 *SE*), averaged over 15 participants, is plotted as a function of subjective visibility rating. The dashed line represents chance performance. For Experiment 2 (b), the mean nonsymbolic priming effect (±1 *SE*) from invisible stimuli, averaged over 17 participants, is plotted as a function of the numerical distance between the prime and target. For Experiment 3 (c), the mean symbolic priming effect (±1 *SE*) from invisible stimuli, averaged over 13 participants, is plotted as a function of the numerical distance between the prime and target. In (b) and (c), a negative target-prime distance indicates a prime larger than the target; a positive target-prime distance indicates a prime smaller than the target. Priming effects were calculated by subtracting reaction time in the baseline, no-prime condition from reaction time at each distance level. Thus, positive priming effects indicate slowed responses relative to baseline (interference), and negative effects indicate speeded responses (facilitation).

was significant, $F(2, 28) = 20.74$, $p < .001$. At the lowest (0) rating level (i.e., when participants denied any awareness of the prime set), forced-choice enumeration accuracy was at chance level (33%; one-sample *t* test, $p > .1$). Within-participants tests (see the Supplemental Material) showed that none of the participants performed better than chance when enumerating items rated invisible (all *p*s > .05). These results confirm that the participants could not explicitly and directly enumerate the suppressed prime set in the absence of awareness.

Experiment 2

This experiment investigated the influence of an invisible nonsymbolic prime on response to the target quantity. Data from 4 participants were excluded from the analysis (see the Supplemental Material for exclusion criteria). In the remaining 17 participants, on average, the prime set was rated 0 in 64% of trials, 1 in 21% of trials, and 2 in 15% of trials.

With three numerosity levels for the target and prime sets, five different target-prime distances (i.e., target – prime) were possible: –2, –1, 0, 1, and 2. Focusing on invisible-prime trials, we first calculated the priming effect at each distance level for each participant by subtracting the average reaction time (RT) in the correctly enumerated trials at that level from the average RT in the baseline, no-prime condition. A one-way ANOVA showed a highly significant effect of target-prime distance, $F(4, 64) = 7.719$, $p < .0001$ (Fig. 2b). In addition, the direction of the priming effect depended on target-prime distance: For negative distances (i.e., prime larger than target), enumeration was significantly slowed relative to the no-prime baseline. Conversely, for zero and positive distances, enumeration was significantly speeded (see the Supplemental Material for detailed statistics). There was also a trend for the priming effect to be stronger for positive distances than for 0 distance (i.e., identity priming). However, direct comparison of the priming effect at 0 distance with the priming effect at other distances showed a significant difference only for a distance of –2 (paired *t* test), $t(16) = 3.03$, $p = .008$ ($p > .1$ for all other nonzero distances). Additional analysis ruled out the possibility that the effect of target-prime distance on RT was confounded with an effect of target numerosity (see the Supplemental Material).

Experiment 3

This experiment investigated the influence of an invisible symbolic prime on response to the target quantity. Applying the same criteria as in Experiment 2, we excluded data from 5 participants. On average, visibility was rated 0 in 78% of trials, 1 in 8% of trials, and 2 in 14% of trials. For the invisible-prime trials, a one-way ANOVA showed a significant main effect of target-prime distance on the priming effect, $F(4, 48) = 2.6$, $p = .04$. As Figure 2c illustrates, the pattern found in the nonsymbolic condition (Experiment 2) was replicated. Although the general pattern of results was identical to that in Experiment 2, only for one distance level (target-prime distance = +2) was the magnitude of the priming effect individually significant (one-sample *t* test, comparison with zero), $t(12) = -2.419$, $p = .03$. Direct comparison of the priming effect at target-prime identity with the priming effect at other distances did not show any significant differences (all *p*s > .1).

To directly compare the data from Experiments 2 and 3, we conducted a combined analysis with prime notation (i.e., experiment) and target-prime distance as factors. This analysis showed a significant main effect of target-prime distance ($p < .001$; see the Supplemental Material), but significant effects were not found for prime notation or for the interaction of prime notation and target-prime distance. Responses were faster when the prime was smaller than the target than when the prime was larger than the target. Thus, in both experiments, we identified the same pattern, albeit more consistently in Experiment 2.

Experiments 4 and 5

Data from 3 participants were excluded in the analyses of Experiments 4 and 5. In Experiment 4, visibility of the monocular prime was rated 0 in 94% of trials, 1 in 5% of trials, and 2 in 1% of trials. In Experiment 5, visibility of the monocular prime was rated 0 in 86% of trials, 1 in 11% of trials, and 2 in 3% of trials. Thus, masking by CFS proved to be very effective. With binocular primes, 65% (Experiment 4) and 68% (Experiment 5) of the primes were rated 2, 7% (Experiment 4) and 11% (Experiment 5) were rated 1, and 28% (Experiment 4) and 21% (Experiment 5) were rated 0.

Figure 3a shows the priming effect of invisible stimuli in Experiment 4. A one-way ANOVA revealed a significant main effect of target-prime distance on the priming effect, $F(4, 60) = 4.50$, $p = .003$; the main effect found in Experiment 2 was replicated (cf. Fig. 2b). As in Experiment 2, the priming effect depended on target-prime distance: For the larger negative target-prime distance, RTs were slowed relative to the no-prime baseline, whereas for positive target-prime distances, RTs were faster relative to the baseline (see the Supplemental Material for details). Unlike in Experiment 2, the facilitatory priming effect for the largest distance (+2) did not reach the chosen level of significance. This difference between the experiments could have been due to deeper suppression of the prime set in Experiment 4 (as a result of reduced prime contrast and duration). As in Experiment 2, direct comparison of the priming effect at target-prime identity with the priming effect at other distances (paired *t* tests) revealed a significant difference for the target-prime distance of –2, $t(15) = 3.57$, $p = .019$, and a marginally significant difference for the distance of –1, $t(15) = 2.08$, $p = .054$, but no significant differences for the positive distances ($p > .8$).

Figure 3b shows the effect of a consciously perceived prime on enumeration RT for each level of target-prime distance in

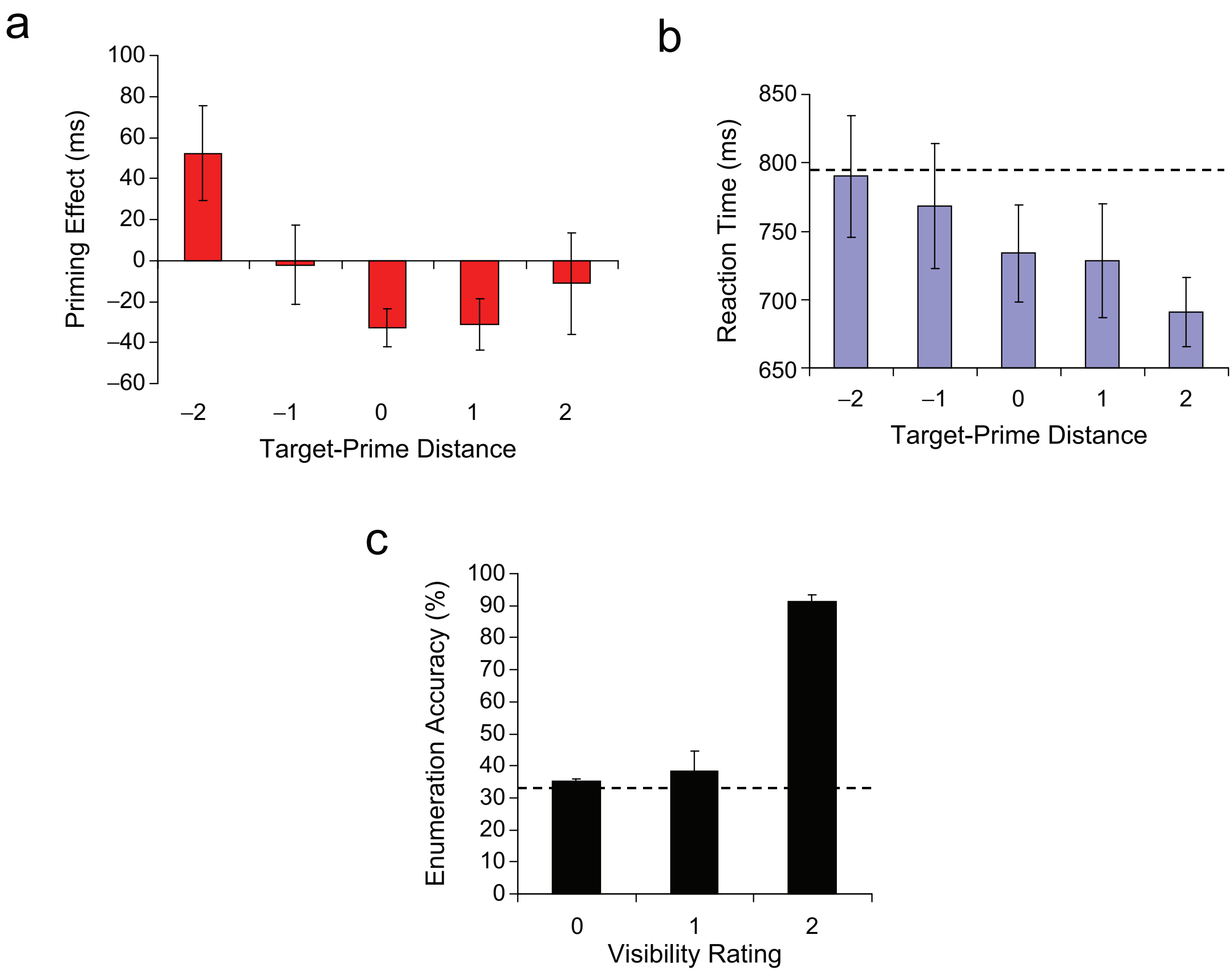

Fig. 3. Results from Experiments 4 and 5. In (a), the mean nonsymbolic priming effect from invisible stimuli (±1 *SE*) in Experiment 4 is plotted as a function of the numerical distance between the prime and target. A negative target-prime distance indicates a prime larger than the target; a positive target-prime distance indicates a prime smaller than the target. Priming effects were calculated by subtracting mean reaction time in the baseline, no-prime condition from mean reaction time at each distance level. Thus, positive priming effects indicate slowed responses relative to baseline (interference), and negative effects indicate speeded responses (facilitation). In (b), mean reaction time following visible primes (±1 *SE*) in Experiment 4 is plotted for each target-prime distance. The dotted line represents the mean reaction time in the baseline, no-prime condition. (See the Supplemental Material available on-line for an explanation of why reaction times, rather than priming effects, have been plotted.) The graph in (c) presents mean enumeration accuracy for the prime set (±1 *SE*) in Experiment 5 as a function of subjective visibility. The dashed line represents chance performance. Data are averaged over 16 participants.

Experiment 4. A one-way ANOVA revealed a significant main effect of target-prime distance, $F(4, 60) = 7.11$, $p < .0001$. These results showed that target-prime distance affected enumeration RT in a qualitatively similar manner regardless of whether the prime was perceived consciously or unconsciously. However, direct comparison of RTs at target-prime identity with RTs at other distances (paired *t* tests) showed a significant difference for the target-prime distance of –2, $t(15) = 3.31$, $p = .005$, and for a distance of +2, $t(15) = 3.308$, $p = .005$, implying that the distance effect was stronger when the prime was visible than when it was invisible. Conscious perception of the prime speeded up RTs (see the Supplemental Material) relative to the no-prime condition (see Fig. 3b), masking the interference effect that was previously observed for unconsciously perceived primes in the negative-distance conditions. It is likely that the interfering effect of the numerosity of the prime was balanced by the alerting effect of the prime when it was visible.

In Experiment 5, accuracy in enumerating the prime set increased with visibility rating, $F(2, 30) = 73.82$, $p < .001$ (Fig. 3c); thus, the results of Experiment 1 were replicated. Accuracy for forced-choice enumeration was not different from chance for primes rated invisible ($p > .1$). Within-participants tests (see the Supplemental Material) showed that only 2 out of 16 participants departed from chance in accuracy of enumerating items rated invisible, but the comparison with chance did not reach significance for these 2 participants after correction for multiple comparisons.

Finally, an additional analysis of data from Experiments 2 through 4 was performed by collapsing the data from corresponding positive and negative target-prime distances, to examine the priming effect as a function of absolute target-prime distance (i.e., 0, 1, or 2). A significant, positive unconscious priming effect (i.e., interference) that increased with absolute target-prime distance was found only in the case of nonsymbolic primes and nonsymbolic targets (Experiments 2 and 4), but not in the case of symbolic primes and nonsymbolic targets (Experiment 3; see the Supplemental Material for details).

Discussion

In five experiments, we investigated numerical processing of small quantities (1–3) that were inaccessible to awareness as a result of interocular suppression. Experiment 1 showed that participants could not explicitly and directly enumerate items that did not reach conscious awareness. We then showed that both nonsymbolic (Experiment 2) and symbolic (Experiment 3) unconsciously perceived primes induced a robust distance-dependent priming effect. Comparison with a no-prime baseline indicated that primes larger than targets interfered with target enumeration. Conversely, primes identical to or smaller than targets facilitated target enumeration. The effects of luminance, prime surface area and orientation variability, and target magnitude per se were controlled and so cannot explain our findings. Experiments 4 and 5 replicated Experiments 1 and 2 within a single group of participants, and showed that the priming effect was robust to deep suppression. Finally, conscious priming effects induced by visible primes were also demonstrated. RTs to the target depended strongly on the target-prime distance in a manner consistent with and similar to the effect observed when primes were unconsciously perceived. In addition, visible primes accelerated enumeration in general, presumably by alerting participants to the imminent appearance of the target.

Implications for consciousness

Taken together, these results demonstrate unconscious high-level priming specific to the quantity relationship between target and prime despite interocular suppression of the prime. Previous behavioral investigations of priming in binocular rivalry (Cave et al., 1998; Zimba & Blake, 1983) suggested that unconscious monocular primes are incapable of high-level priming. These findings led to the proposal that awareness is necessary for higher-level cognitive stages of visual processing, such as picture naming and lexical decision (Blake & Logothetis, 2002). A more recent study (Jiang, Costello, & He, 2007) showed that upright faces and words written in a learned alphabet break through suppression faster than inverted faces and words written in an unlearned alphabet. This finding led to the hypothesis that visual information suppressed by interocular suppression may be sufficient to activate higher-level cognitive processing stages.[1] Our results provide striking evidence supporting this hypothesis and contradicting the notion that high-level cognitive processing—such as appreciation of numerical quantity that is dissociated from luminance, surface area, and feature (e.g., orientation) variability—is necessarily eliminated by interocular suppression.

Unlike studies using interocular suppression (Cave et al., 1998; Zimba & Blake, 1983), those involving masked priming paradigms have repeatedly demonstrated high-level subliminal priming (Marcel, 1983). An important conclusion from the latter studies is that such priming effects are highly task dependent (Dehaene & Naccache, 2006). Therefore, previous negative findings may have resulted from use of suboptimal tasks. In particular, picture naming (Cave et al., 1998) and lexical decision (Zimba & Blake, 1983) are ostensibly linked to ventral visual pathways (Cohen et al., 2000; Grill-Spector, Kourtzi, & Kanwisher, 2001). We hypothesized that an unconscious prime may induce priming effects, despite interocular suppression, in an enumeration task. This hypothesis rested on findings that images of tools rendered invisible by interocular suppression can effectively drive brain regions responsive to visual-spatial action (Fang & He, 2005), and that these same brain regions are also strongly involved in numerical cognition (Hubbard et al., 2005). The present results confirm our prediction that unconscious priming effects during interocular suppression may be demonstrated with a task—such as enumeration—that is directly linked to parietal cortex.

More recently, another study (Almeida, Mahon, Nakayama, & Caramazza, 2008) showed category-specific unconscious priming of object recognition by images of human-made tools (which are particularly preferred by the dorsal visual stream; Fang & He, 2005) rendered invisible by CFS. Object priming despite CFS was independent of the task type and was absent for images of animals (presumably preferred by the ventral stream), which suggests that stimulus-specific dorsal-stream sensitivity to tool images may have been necessary for object priming. The distance effect demonstrated in our experiments goes beyond mere semantic categorization, showing that detailed information about quantity is preserved and transmitted despite CFS.

Another difference between the current study and previous work (Cave et al., 1998; Zimba & Blake, 1983) concerns the mechanism of suppression. Previous studies relied on presenting the unconscious prime to the suppressed eye during the perceptual fluctuations of binocular rivalry, but we employed CFS to render the primes invisible. Compared with binocular rivalry, CFS offers both stronger masking and more precise and deterministic control over subjective experience (Fang & He, 2005; Kim & Blake, 2005; Tsuchiya & Koch, 2005). Although suppression by CFS and rivalry share many features, they are not necessarily identical (Tsuchiya, Koch, Gilroy, & Blake, 2006), and they may affect priming in different ways. Further research involving direct comparison of priming under CFS and under rivalry is needed to clarify the role of the method of suppression on unconscious interocular priming.

Implications for numerical cognition

We found that explicit enumeration of nonsymbolic items (i.e., the target set) could be primed by unconscious nonsymbolic or symbolic numerosities. Previous failures to demonstrate unconscious nonsymbolic priming in normal healthy participants (Koechlin et al., 1999) contrast with findings that some neglect patients can enumerate small nonsymbolic quantities displayed in their "unaware," extinguished left hemifield (Vuilleumier & Rafal, 2000). Our results resolve this apparent discrepancy by showing that if the task and numerosity range are similar to those used in the patient study (Vuilleumier & Rafal, 2000), then nonsymbolic quantities are indeed capable of priming nonsymbolic enumeration in healthy participants, too.

Previous work on numerical priming focused on target-prime distance and did not employ a no-prime condition as a baseline (Koechlin et al., 1999; Reynvoet & Brysbaert, 1999, 2004; Reynvoet, Brysbaert, & Fias, 2002; Roggeman et al., 2007). The data presented here go beyond those earlier studies by including a no-prime baseline that permitted us to disentangle the facilitating or interfering effects of the prime on the target.

We observed that the direction of the target-prime distance profoundly affected the nature of the priming effect. We found strong interference for negative distances, relative to the no-prime baseline, and a somewhat smaller but nevertheless very consistent facilitation for positive distances; these effects were observed for both nonsymbolic (Experiment 2 and 4) and symbolic (Experiment 3) primes, although they were much more consistent when the prime and target set shared the same nonsymbolic notation. These results are counterintuitive, but not inconsistent with previous behavioral findings: When comparing two consecutively presented symbolic (Kaan, 2005) or nonsymbolic (Paulsen & Neville, 2008) quantities, participants are faster and more accurate if the sequence increases rather than decreases. It is important to note that the asymmetry we observed excludes response-selection conflict/congruency as an alternative explanation of the results. Target-prime distances of opposite sign should show similar and symmetric effects of response-selection conflict, which is clearly not the case in our data.

In addition, pooling the data from corresponding negative and positive distances showed that interference increased with absolute target-prime distance. Although such a pattern of results is more familiar in the case of classic numerical priming effects (e.g., Koechlin et al., 1999), our analyses underscore the relevance of the sign of target-prime distance in numerical priming. Collapsing trials into absolute-distance bins could mask important variability in the data, namely, the opposite direction of priming for positive and negative distances (Experiments 2 and 4) and, even more important, the effect of symbolic primes on enumeration of nonsymbolic targets (Experiment 3).

Our data also showed that in some cases (e.g., distance = +2 in Experiment 2), there was a trend for somewhat larger priming effects when the prime was not the same as the target than when the prime and target were the same. In contrast, experiments with nonnumerical primes have shown that priming effects are typically strongest when the prime and target are the same. One possible reason for the difference between results is that the effects we observed reflect the superposition of opposing order-dependent and distance-related processes. Consistent with this idea, recent work on the relationship between numerical order information and quantity information has shown that different cognitive mechanisms underlie quantity and order judgments (Turconi, Campbell, & Seron, 2006). Specifically, the classic distance effect is modulated by numerical order (ascending vs. descending) in an order judgment task. Although our task did not involve explicit order judgments, participants had to perform sequential tasks (enumeration and visibility rating) on sequentially presented stimuli (target and prime). Another recent study has shown asymmetric numerical (conscious) priming effects across prime-target distance (Roggeman et al., 2007), but the direction of the effects was opposite to the direction in our experiments and those of Turconi et al. (see the Supplemental Material for a detailed comparison). These studies and other recent work (Van Opstal, Gevers, De Moor, & Verguts, 2008) point to the existence of multiple cognitive processes underlying numerical judgments.

Previously found dissociations between the effects of symbolic and nonsymbolic primes in numerical priming (Koechlin et al., 1999; Roggeman et al., 2007) have been attributed to a theoretical model in which digits activate *place coding*, whereby adjacent numbers are represented as overlapping activations on a mental number line, whereas dots activate *summation coding*, whereby activation increases in proportion to the number of dots (Verguts & Fias, 2004). In contrast, our results show very similar patterns for dot and digit priming. These results are compatible with the kind of summation model proposed by Zorzi and his colleagues (Zorzi & Butterworth, 1999; Zorzi et al., 2005), which they term *numerosity coding*. In this model, both symbolic and nonsymbolic numbers are mapped onto a common summation code in discrete cardinal steps.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interests with respect to their authorship and/or the publication of this article.

Funding

This work was supported by the Wellcome Trust (G. Rees) and the European Commission (B. Bahrami, P. Vetter, and B. Butterworth).

Supplemental Material

Additional supporting information may be found at http://pss.sagepub.com/content/by/supplemental-data

Note

1. However, inferring a semantic level of unconscious processing from this result would be hazardous, as the same finding could also be expected from accumulation of low-level information together with a lower threshold for the more familiar categories (upright faces and meaningful words).

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