

- In both intrahelical platforms (J6/6a and J6a/6b), strong density in the $F_o - F_c$ electron density map is consistent with a metal ion or water molecule in the major groove coordinated to the ribose and phosphate of the 5' A and 3' A of the platform, respectively, and to N7 and O6 of the G in the G-U wobble below the motif. In the L5c loop platform, however, there is density for a putative magnesium ion coordinated to phosphates of the 3' A of the platform and the adjacent A of the A-U noncanonical pair. Both molecules in the asymmetric unit reflect these differences between the platforms.
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 14. The J6a/6b paired mutant has U224-A225-A226 converted to an A-U dinucleotide, causing it to base pair with the A-U across the loop. It showed a cleavage rate of $0.006 \pm 0.003 \text{ min}^{-1}$ (mean $\pm$ range of four experiments) with 100 nM of each domain, a concentration that is nearly saturating for the wild-type components ($K_{1/2} = 31 \text{ nM}$ for P4-P6 and 4 nM for P3-P9). The J6/6a paired mutant has C217-A218-A219 converted to the sequence U-G-C, causing it to base pair with the G-C-A across the loop. It showed a cleavage rate of $0.0166 \pm 0.0004 \text{ min}^{-1}$ under the conditions described above. Wild-type P4-P6 gave a rate of $0.43 \pm 0.04 \text{ min}^{-1}$ in side-by-side experiments. Preliminary RNA splicing analysis of a precursor RNA with a two-base change in the third adenosine platform, A171-A172 to U-U, showed a twofold reduction in activity at low magnesium ion concentration (5 mM) and even less of an effect at higher magnesium concentrations. One example each of potential C-U and U-C platforms occurs in the tetraloop receptor motif of group I introns in subclasses IC1 and IC3.
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Three Cognitive Markers of Unconscious Semantic Activation

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A "response window" technique is described and used to reliably demonstrate unconscious activation of meaning by subliminal (visually masked) words. Visually masked prime words were shown to influence judged meaning of following target words. This priming-effect marker was used to identify two additional markers of unconscious semantic activation: (i) the activation is very short-lived (the target word must occur within about 100 milliseconds of the subliminal prime); and (ii) unlike supraliminal prime-target pairs, a subliminal pair leaves no memory trace that can be observed in response to the next prime-target pair. Thus, unconscious semantic activation is shown to be a readily reproducible phenomenon but also very limited in the duration of its effect.

Demonstrations of judgments or actions being influenced by unperceived stimuli (1) have both interesting and uninteresting possibilities for interpretation. The uninteresting possibility is that perceptual measurements have been insensitive—the critical stimuli may have been perceived, but the research apparatus or procedure failed to

register that perception. The more interesting—but also controversial—possibility is that stimulus-triggered cognition has indeed occurred without conscious perception of the initiating stimulus. Tests of the hypothesis of unaware perception date from the late 19th century (2). When claims of analysis of semantic information from unperceived stimuli were strongly pressed in the second half of the 20th century (3), methodological critiques (4) of the adequacy of evidence for such claims resulted in widespread skepticism about those claims.

In this controversial domain, experi-

mental work of the past two decades has focused on claimed findings of subliminal semantic activation (5)—the claim that word meanings are analyzed when words are presented so as to evade conscious perception. Subliminal semantic activation is most often investigated with priming procedures. Subjects perform a two-choice categorization task that is supplemented by the presentation of a subliminal prime word shortly before each to-be-judged target stimulus word. The two categorization tasks that have been used most often for tests of subliminal priming have the subject decide whether or not a target letter string forms a word (6) or whether a target word is pleasant or unpleasant in meaning (7). Priming is said to occur when the meaning of the prime affects the speed or accuracy of response to the target. Priming is given the controversial label "subliminal" if it occurs when the prime is visually masked to reduce or eliminate conscious perception (8).

Despite numerous empirical demonstrations, subliminal priming has remained a controversial phenomenon because (i) reported findings have been statistically weak, (ii) it has been difficult to provide convincing evidence that visually masked prime words are indeed not consciously perceived, (iii) published replications are rare, and (iv) many active investigators have accumulated multiple unpublished and unsuccessful attempts to replicate their own or others' published findings. Against this background of empirical difficulty, Draine and Greenwald (9) recently described a "response window" procedure that, in combination with visual masking procedures that can be implemented easily on standard computer displays, reliably produces statistically strong subliminal priming effects. Here we use the response window procedure to establish a few empirical properties of subliminal semantic priming.

Subjects (10) performed a categorization task either for affectively polarized words (to be categorized as pleasant or unpleasant in meaning) or for common first names (to be categorized as male or female). In different conditions within each experiment, the interval between start of prime and start of target stimulus—an interval referred to as the prime-target stimulus onset asynchrony (SOA)—was varied through values that ranged from 67 to 400 ms. Subjects were assigned to either subliminal or supraliminal priming according to a counterbalancing scheme that also systematically varied both the order in which SOA values appeared and which of the two item sets (male or female names, pleasant or unpleasant words) was used in the priming task. Each subject provided indirect measure (priming) data for two or three 50-trial blocks at each SOA

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value used in an experiment (11). Direct measures of prime perceptibility were obtained from separate (later) blocks of trials for which instructions described the pre- and postmasking procedure and asked subjects to make various discriminations of content for the visually masked stimuli (12).

Results from several response-window experiments are summarized as regression functions that relate priming to measures of perceptibility of the primes (Fig. 1). When such regression analyses use priming and perceptibility measures for which zero values indicate absence of priming and perceptibility, respectively, the height at which the function crosses the vertical axis (the regression intercept) provides a critical test of the hypothesis that priming has occurred unconsciously. The regression intercept estimates the magnitude of priming associated with zero perceptibility of the prime. When this priming magnitude is significantly greater than zero, there is evidence for unconscious semantic activation (13). In Fig. 1, intercepts of the regression functions were statistically significant for all three prime durations (17, 33, and 50 ms).

Additional experiments were performed in which 50-ms primes were presented either with pre- and postmasking, making them subliminal for most subjects (14), or with no masking, making them supraliminal (that is, visible). In these experiments (Fig. 2), subliminal priming was generally weaker than supraliminal priming. More importantly, however, the shapes of functions relating magnitude of priming to prime-target SOA were sharply different for supraliminal and subliminal priming. Supraliminal priming was consistently strong, perhaps even increasing in strength, across SOAs varying from 100 to 400 ms. By contrast, subliminal priming was moderated substantially by SOA, being consistently strong only at a very short SOA (67 ms) and decreasing to low levels for SOAs longer than 100 ms. The results shown in Fig. 2 reveal that the temporal span of subliminal priming is very brief in comparison with that of supraliminal priming. In retrospect, these findings demonstrate why subliminal priming has been such an elusive phenomenon in previous research: Virtually all previous studies of subliminal priming have used SOAs that exceeded 250 ms. By contrast, Fig. 2 shows that subliminal priming is readily obtainable only with SOAs of 100 ms or less.

Another empirical pattern (Fig. 3) was found to differentiate subliminal from supraliminal priming. For supraliminal priming, magnitude of priming was affected by the relation between prime and target stimuli on the just-preceding trial. When the preceding trial was an incongruent prime-target pair, supraliminal priming was weaker than when

the preceding trial was a congruent pair. This finding indicates that impact of the prime was affected by its recent usefulness (that is, the prime-target congruency), but only for visible primes; that is, supraliminal (visible) primes were more potent in facilitation or interference on the trial just after one on which the prime and target had been congruent, compared to one on which they had been incongruent. This pattern indicates a form of memory for the preceding trial's prime-target configuration. By contrast, magnitude of subliminal priming was unaffected by the congruency or incongruency of the preceding prime-target pair; that is, subjects gave no evidence of retaining information about the most recent prime-target configuration (15).

The findings in Figs. 1 to 3 collectively establish a convergence of stimulus presentation operations and cognitive indicators that define unconscious semantic activation in the semantic priming experiment. The chief defining operation is the use of visual masking to produce low levels of prime perceptibility. The defining cognitive indicators of subliminal semantic activation are the data patterns shown in Figs. 1 to 3: (i) a significant intercept effect in the regression of measures of priming on measures of the prime stimulus's perceptibility, (ii) limitation of subliminal priming to target stimuli that occur within about 100 ms of the visually masked primes, and (iii) absence of any effect of the preceding trial's prime-target congruence on magnitude of

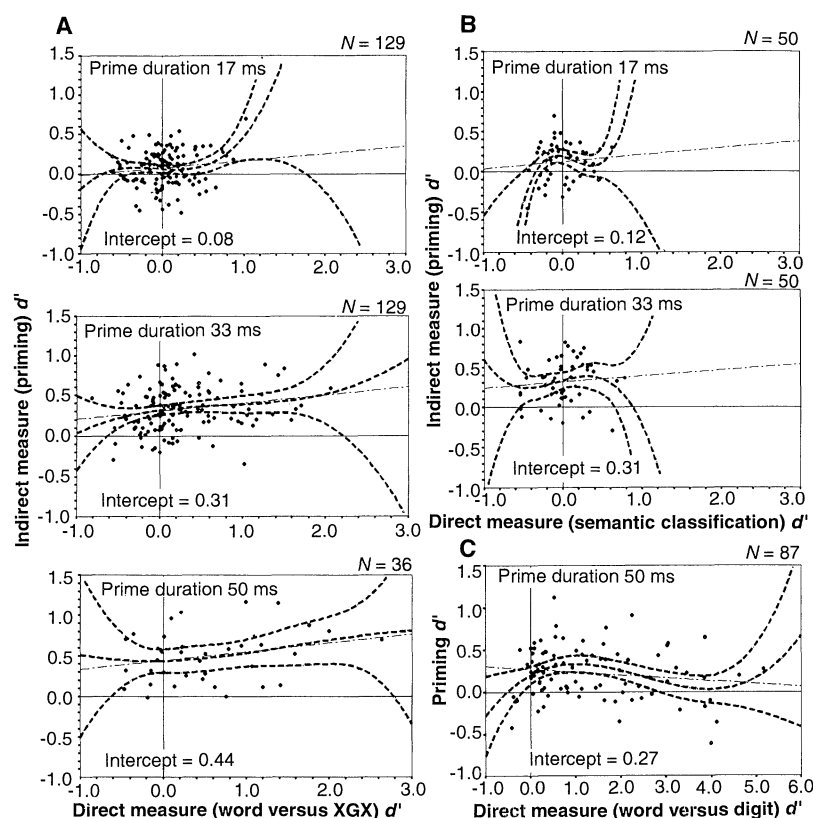


Fig 1. Magnitude of priming as a function of performance on direct measures of prime perceptibility. Each scatterplot point represents an individual subject's average performances at both priming and direct-measure tasks at the indicated prime duration. Each plot shows both a best-fitting cubic regression function with its 95% confidence interval (22) and a superimposed linear regression function. (A and B) Data are from 67-ms SOA masked-priming conditions of experiments reported by Greenwald and Draine (9, 21), and (C) from two additional experiments that included conditions with 50-ms prime durations and 67-ms SOAs (23). Direct measures of prime perceptibility are from separate (later) blocks of trials on which subjects were asked to discriminate either lexicality [whether stimuli presented between premask and postmask were (A) words versus strings of alternating X's and G's (for example, XGXGX) or (C) words versus digits] or semantic meaning [whether masked stimuli were (B) words of pleasant versus unpleasant meaning or male versus female first names]. Sensitivity (d') values for direct measures were computed by treating one category (for example, words) as signal and the other (for example, digits) as noise, such that guessing word in response to a digit stimulus would be treated as a false alarm. Indirect measure (priming) d' values were computed by scoring a hit when (say) a male-name response was given on a trial with a male-name prime, and a false alarm when a male-name response was given on a trial with a female-name prime. Printed numerical intercepts are those for the linear regression in the panel; N , number of subjects (scatterplot points).

priming. Figures 2 and 3 show that the latter two findings for subliminal priming are markedly different from the data patterns obtained for priming by visible words.

These findings relate closely to two long-established categories of findings: (i) The central nervous system monitors stimuli outside its current focus of attention, as evidenced (for example) by humans' facility in switching attention to a previously unattended sensory channel when important or unexpected content appears in that channel (16); and (ii) visual backward masking (postmasking) interrupts processes that are understood as the transfer of information from a sensory buffer to working memory. Both of these findings were central to the information-processing paradigm, developed in the 1950s and 1960s, that started the modern era of cognitive psychology (17).

Stated in terms borrowed from the information-processing era, one can understand the postmask as interrupting transfer of information about the prime stimulus from sensory buffer to working memory. (In the older paradigm, working memory was sometimes interpreted as an equivalent of conscious awareness.) This hypothesized interruption of transfer explains both the lack of conscious perception of the prime and its lack of persisting effects, particularly the

absence of any effect of prior-trial prime-target congruence on current-trial magnitude of priming (Fig. 3). Although the postmask disrupts conscious perception of the prime, it does not prevent semantic activation. The occurrence of semantic activation by consciously unperceived primes indicates that this semantic activation does not depend on the prime reaching working memory (awareness). However, this semantic activation is shown to be a very evanescent phenomenon by the sharply decreasing function (Fig. 2) that relates subliminal priming to SOA (18).

The rapidity of the rise and fall of subliminal semantic activation described here exceeds even the briefest persistence previously demonstrated in cognitive psychology—the approximately 250-ms persistence of unattended visual sensory memory in light-adapted observers (19). Although this approximately tenth-of-a-second flicker of subliminal semantic activation has been described here as a property of stimuli that do not achieve conscious awareness, it remains possible that it is also a property of visible stimuli that are masked after a brief presentation. Findings obtained with mutually masking rapid successions of visible stimuli similarly suggest a brief duration of semantic activation (20).

Fig. 2. Magnitude of subliminal and supraliminal priming as a function of prime-target SOA. The measure of priming is the same signal-detection measure of sensitivity of target responses to prime meaning shown in Fig. 1. Error bars give 95% confidence intervals. Data are from experiments in which (A) both supraliminal and subliminal priming were measured and (B) only subliminal priming was measured. Prime duration was constant at 50 ms in all experiments. The results show supraliminal priming to be obtained strongly at SOAs as long as 400 ms, whereas subliminal priming decreased sharply at SOAs >100 ms.

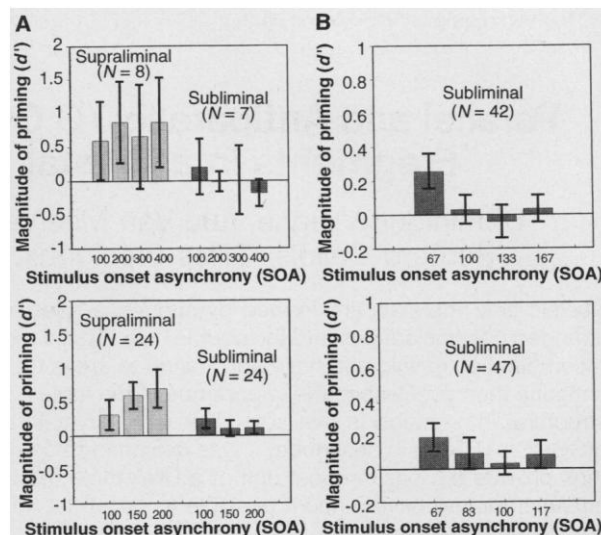
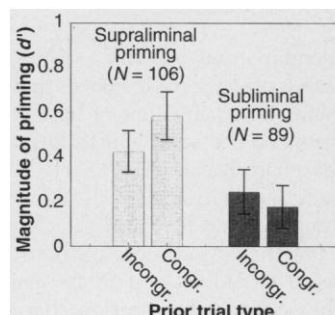


Fig. 3. Magnitude of priming after immediately prior congruent versus incongruent priming trials. Priming magnitudes are presented in the same format as those in Fig. 2. The supraliminal priming data are from nonmasked conditions in which prime duration was 50 ms and SOA was 150 ms, whereas the subliminal priming data are from visually masked conditions that produced largest subliminal priming effects (prime duration = 50 ms, SOA = 67 ms). The results show that for supraliminal priming (but not subliminal priming), a prior incongruent trial weakens priming relative to a prior congruent trial.



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9. A. G. Greenwald and S. C. Draine, paper presented at the 36th Annual Meeting of the Psychonomic Society, Los Angeles, CA, 10 to 12 November, 1995.
10. Subjects, all of whom were University of Washington undergraduates, gave consent to participation after having read a preliminary description of experimental procedures.
11. On each trial of the task, a prime word (either a male or female name, or a pleasant or unpleasant word) was briefly displayed and, after a variable short delay, the target word (a different first name or a different affectively polarized word) was presented. Prime and target words were randomly selected on each trial with two constraints: (i) no target was presented twice in any block of 50 trials, and (ii) the proportion of congruent trials (prime and target having the same affective meaning, or prime and target having the same name gender) was constrained to an average of 50%. One hundred different stimuli (words or names) were used for each categorization task. In each task one subset of 50 served as primes and the remaining 50 served as targets, with these assignments appropriately counterbalanced across subjects. Examples of stimuli are as follows: unpleasant (vomit, kill, bomb), pleasant (honor, happy, kiss), male (mike, david, kevin), and female (kate, mary, sarah). The subject's instructed task was to classify the target word by pressing a key on the left or right side of a computer keyboard (for example, left key to indicate unpleasant and right key for pleasant). After a few blocks of 10 to 20 trials each for practice with the categorization task, subjects started to practice producing their responses during a "response window" that was initially established as the interval from 383 to 517 ms after start of presentation of the target word. Some of the experiments took advantage of speed-accuracy trade-offs [W. A. Wickelgren, *Acta Psychol.* **41**, 67 (1977); B. A. Doshier, *Cognit. Psychol.* **13**, 551 (1981)] by shifting the term-

poral position of the response window to a shorter or longer value, depending on the subject's ability to perform (for example, shortening it if subjects were making few errors). The response window procedure obliged subjects to respond at speeds that did not permit high levels of accuracy and, consequently, error rates were substantial. (Mean latencies of highly motivated subjects under instructions to respond rapidly are typically between 550 and 650 ms.) The production of relatively high error rates allowed the priming effect—that is, the effect of the prime's congruence versus incongruence with the target's meaning—to be observed in subjects' error rates rather than in their response latencies to targets. With this response window procedure, priming took the form of lower error rates for congruent priming than for incongruent priming, reflecting some combination of facilitation by congruent primes and interference by incongruent primes. Priming was therefore measurable by observing the difference between these error rates. Even though the procedure was designed to constrain response latencies to approximately the range of values that define the response window, response accuracy was analyzed for all trials except for a small percentage with latencies greater than 1500 ms, a value substantially longer than the time elapsed at the end of the window interval. The primary measure used with these data was signal detection theory's d' measure of sensitivity of the target word's response to the prime word's meaning [see the further explanation in the legend to Fig. 1, and D. M. Green and J. A. Swets, *Signal Detection Theory and Psychophysics* (Wiley, New York, 1967)]. Results for this sensitivity measure were similar to those obtained with various alternative measures, such as the increase in error rate for incongruent relative to congruent primes or measured information transmitted from prime stimulus to target response. Prime words were presented for 17, 33, or 50 ms at a centered display location to which subjects were instructed to attend. In the visually masked (subliminal) prime condition, the prime was both preceded and followed, at the same screen location, by strings of consonants that served as forward mask (premask) and backward mask (postmask). (An example of a mask stimulus is the letter string GKQHYTPDGFQBYLG.) The pre-mask, prime, postmask, and target stimuli were presented as black letters on a gray background. The pre-mask lasted 100 ms and the postmask 17 ms. (Other pilot studies had shown that masking effectiveness was unaltered by increases in postmask duration beyond 17 ms, the minimum value obtainable with the 60-Hz computer display used in this research.) Subjects viewed the computer video display through a device that presented images from left and right halves of the display screen separately to left and right eyes. Although this dichoptic presentation was not needed for the present procedures (which presented identical stimuli to both eyes at all times), its use has been found to increase mildly the effectiveness of visual masking. The combination of premask and postmask made the prime words difficult or impossible to see for almost all subjects. By contrast, in supraliminal conditions the masking consonant strings were replaced by blanks (that is, the screen background color), as a consequence of which the prime words were easily legible despite their short (50 ms) duration.

12. Because preliminary findings revealed that direct measure performance was depressed by the requirement to respond rapidly, the response window procedure was not used during blocks of trials that obtained direct measures. Different discriminations on visually masked stimuli were requested in different experiments to allow opportunities to demonstrate that some types of information might penetrate visual masking more readily than others. The basic properties of the results shown in Fig. 1 did not vary with the different direct measures, adding to confidence in generality of conclusions.
13. The conclusion that unconscious cognition is indicated by the presence of statistically significant intercept effects in the regression analyses of Fig. 1 rests on a methodological analysis by A. G. Greenwald, M. R. Klinger, and E. S. Schuh [*J. Exp. Psychol. Gen.*

- 124, 22 (1995)] that extends the logic of an analysis introduced by P. M. Merikle and E. M. Reingold [*J. Exp. Psychol. Learn. Mem. Cognit.* 17, 224 (1991)]. A concern in interpreting such intercept effects is the possibility that a spurious intercept may be produced when the predictor (in this instance, the direct measure of prime perceptibility) is imperfectly measured. However, the regression analyses in Fig. 1 do not have the properties that can produce such spurious intercept effects. Such properties include both positive regression slopes and average predictor scores substantially above zero. In contrast, the regression slopes that we obtained were approximately flat and predictor scores (that is, direct measures) were noticeably above zero only with prime duration of 50 ms. For a more detailed discussion of the possibility of spurious intercept effects, see (21)
14. The level of perceptibility of masked 50-ms primes can be read from the horizontal distribution of values in the lower panel of Fig. 1, A and C. Levels of direct measure performance corresponding to d' values <1.0 are commonly associated with self-reports of little or no perceptibility. Findings of SOA effects closely resembling those in Fig. 2B were obtained when the plotted variable was changed to magnitude of intercept effect from regression analysis; that is, statistically significant intercept effects were found only for the 67-ms SOA. The intercept-effect alternative analysis confirms that the pattern in Fig. 2B for subliminal priming as a function of SOA is indeed a pattern for unconscious priming. The plotted analysis in Fig. 2B, which includes all subjects who received masked priming, is properly comparable to the analysis in Fig. 2A for supraliminal priming (for which regression analysis is not an appropriate method).
15. The result shown in Fig. 3 is related to one previously reported by J. Cheesman and P. M. Merikle [*Can. J. Psychol.* 40, 343 (1986)]. They showed that supraliminal priming was greater when there was a higher proportion of congruent priming trials in a block of trials, but subliminal priming showed no such effect. Their finding could be explained by the difference in two-trial sequential effects shown in Fig. 3.

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18. The brevity of unconscious semantic activation measured by the prime-target SOA should not be confused with the latency after masked prime presentation at which semantic information is available. Semantic activation is presumed to occur after preliminary operations that may require a few hundred milliseconds for subliminal prime words (as well as for visible target words).
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22. Cubic polynomial regression functions were used to capture possible nonlinear trends in the data. However, it can be seen in the figure that intercept effects for these nonlinear functions were similar to those estimated by linear regression functions.
23. R. L. Abrams, S. C. Draine, A. G. Greenwald, paper presented at the 36th Annual Meeting of the Psychonomic Society, Los Angeles, CA, 10 to 12 November, 1995.
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Parallel and Antiparallel (G-GC)₂ Triple Helix Fragments in a Crystal Structure

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Nucleic acid triplexes are formed by sequence-specific interactions between single-stranded polynucleotides and the double helix. These triplexes are implicated in genetic recombination *in vivo* and have application to areas that include genome analysis and antigene therapy. Despite the importance of the triple helix, only limited high-resolution structural information is available. The x-ray crystal structure of the oligonucleotide d(GGCCAATTGG) is described; it was designed to contain the d(G-GC)₂ fragment and thus provide the basic repeat unit of a DNA triple helix. Parameters derived from this crystal structure have made it possible to construct models of both parallel and antiparallel triple helices.

Combinations of three RNA or DNA strands produce triple helices that have been characterized in terms of base complementarity and the relative orientations of sugar-phosphate backbones (1). Hydrogen bonds are formed between the available functional groups of each base pair in a Watson-Crick double helix and those of the third (Hoogsteen) strand located in its major groove. The sequence recognition that this allows

has been applied in the precise targeting of sequences in double-stranded DNA to exclude DNA binding proteins, including gene promoters (2), from their specific binding sites, and to direct single-site cleavage in chromosomal DNA (3). Triple helix formation has also been presented as a mechanism for alignment of homologous sequences before genetic recombination (4) and may take place *in vivo* (5).