

Imaging unconscious semantic priming

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Visual words that are masked and presented so briefly that they cannot be seen may nevertheless facilitate the subsequent processing of related words, a phenomenon called masked priming^{1,2}. It has been debated whether masked primes can activate cognitive processes without gaining access to consciousness^{3–5}. Here we use a combination of behavioural and brain-imaging techniques to estimate the depth of processing of masked numerical primes. Our results indicate that masked stimuli have a measurable influence on electrical and haemodynamic measures of brain activity. When subjects engage in an overt semantic comparison task with a clearly visible target numeral, measures of covert motor activity indicate that they also unconsciously apply the task instructions to an unseen masked numeral. A stream of perceptual, semantic and motor processes can therefore occur without awareness.

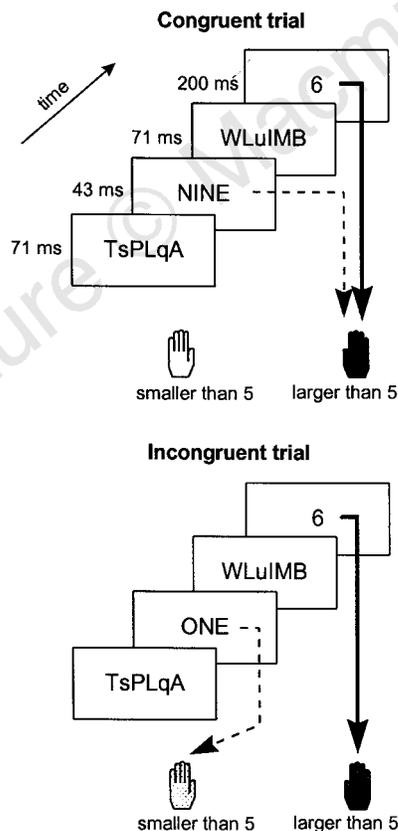


Figure 1 Experimental design. In each trial, the following four visual stimuli appeared successively, centred on the same screen location: a random-letter-string mask, a prime number, another mask, and a target number. Subjects were not informed of the presence of the prime. They were simply told that a 'signal' preceded the target number that they had to classify as larger or smaller than 5. Half of the trials were of the congruent type (prime and target both falling on the same side of 5), and half were incongruent.

We presented a numeral between 1 and 9, the prime, to subjects for a very short duration (43 ms). The prime was masked by two nonsense letter strings, and followed by another numeral, the target (Fig. 1). Under these conditions, even when subjects focused their attention on the prime, they could neither reliably report its presence or absence nor discriminate it from a nonsense string (Table 1). Nevertheless, we show here that the prime is processed to a high cognitive level.

We asked subjects to perform a simple semantic categorization task on the target numeral. Subjects were asked to press a response key with one hand if the target was larger than 5, and with the other hand if the target was smaller than 5. Unknown to them, each target number was preceded by a masked prime which was varied from trial to trial so it too could be larger or smaller than 5. In some trials the prime was congruent with the target (both numbers fell on the same side of 5), and in other trials it was incongruent (one number being larger than 5, and the other being smaller; Fig. 1). We first established that prime–target congruity has a significant influence on behavioural, electrical and haemodynamic measures of brain function. We then showed that the interference between prime and target can be attributed to a covert, prime-induced activation of motor cortex, a response bias that must be overcome in incongruent trials. This indicates that the prime was unconsciously processed according to task instructions, all the way down to the motor system.

The effect of prime–target congruity on behaviour is shown in Fig. 2. Subjects responded more slowly in incongruent trials than in congruent trials ($P < 0.0001$). All 12 subjects showed a positive priming effect, ranging from 2 to 43 ms (average 24 ms, s.d. 13.5 ms). Furthermore, the entire response time distribution was shifted by ~24 ms in incongruent trials compared with congruent trials. Thus, there was no evidence that the effect was found in only a small proportion of subjects or a small number of trials with a distinct distribution of response times.

Two characteristics of the priming effect link it to a semantic level of analysis. First, we varied the notations used for the prime number and for the target number independently. Either number could be presented as an arabic digit (for example, 1 or 4) or as a written word (for example, ONE or FOUR). Although the target notation had a significant main effect on response times ($P < 0.0001$), the amount of priming itself was similar under all conditions of notation and did not interact with target notation, prime notation, or notation change. Priming remained significant even when the notations of the prime and target numbers differed (for example, prime 4, target ONE; $P = 0.0006$). Thus, priming occurred at a notation-independent level of numerical representation⁶. Second, priming remained significant even after trials with repeated numbers (for example,

Table 1 Experimental measures of prime awareness

	Prime duration (ms)					
	0	29	43	57	114	200
Task 1						
Hit rate (%)	4.2	10.4	12.5	25.0	85.4	97.9
False alarms (%)	4.2	7.3	7.3	3.1	5.2	1.0
d'	0.0	0.20	0.30	1.19**	2.68**	4.36**
Task 2						
Hit rate (%)	28.6	40.2	49.1	46.4	78.6	95.5
False alarms (%)	34.8	32.1	41.1	30.4	28.6	16.1
d'	-0.17	0.22	0.20	0.42*	1.36**	2.69**

In two control experiments, subjects were fully informed of the precise structure of the stimuli and were then presented with trials with numerical primes intermixed with trials in which the primes were omitted (explicit detection, task 1; six subjects, 96 trials per cell) or replaced by random strings with the same number of characters (number versus letter-string discrimination, task 2; seven subjects, 112 trials per cell). Prime duration was systematically varied. At the prime duration used in the main experiments (43 ms), subjects consistently reported not seeing the numerical primes (task 1), did not respond differently to prime-absent and prime-present trials (task 1) and were unable to discriminate numerical primes from letter strings (task 2). Discrimination performance, as measured by d' , a bias-free measure of stimulus discriminability derived from signal-detection theory, began to deviate from chance only for a prime duration of 57 ms or more (χ^2 test; asterisk indicates $P < 0.05$; double asterisk indicates $P < 0.001$).

prime ONE, target 1) were excluded from the analysis ($P = 0.001$). Hence, priming did not simply reflect a word repetition effect, but depended on the similarity of the prime and target numbers at a semantic level (larger or smaller than 5).

Event-related potentials (ERPs) recorded during the task also showed a prime–target congruity effect. The central positivity, which culminated at about the time of the subject’s response and is thought to index post-perceptual processing⁷, was delayed by ~24 ms in incongruent trials compared with congruent trials (Fig. 3a). We proposed that the slower responses in incongruent trials might be due to response competition. Subjects would unconsciously apply the task instructions to the prime, would therefore categorize it as smaller or larger than 5, and would even prepare a motor response appropriate to the prime (Fig. 1). In incongruent trials, this prime-induced covert motor activation would mismatch with the overt response required to the target, resulting in response competition and hence slower response times relative to congruent trials.

According to this theory, we should be able to detect an early covert motor activation on the correct response side during congruent trials, and on the incorrect response side during incongruent trials. We tested this prediction using the lateralized readiness potential (LRP), an ERP measure that indexes the activation of lateralized motor circuits⁸ (Fig. 3b). The LRP can detect low levels of covert response activation that do not necessarily result in an overt motor response^{8–10}. As it unfolds in time, the LRP departs from zero as soon as task-relevant information becomes available to bias the motor response towards the left or right hand. Conventionally, positive deflections indicate response preparation on the correct side, whereas negative deflections indicate a transient covert activation on the incorrect response side. Here, the LRP revealed the predicted covert prime-induced motor preparation. In response-locked averages, before the large positive deviation which reflected the activation of motor circuits on the correct response side, the LRP showed a significant difference in the predicted direction between congruent and incongruent trials (one-tailed $P = 0.015$). In incongruent trials, the LRP showed a significant negative deviation (one-tailed $P = 0.005$), indicating motor preparation on the incorrect side of response, whereas in congruent trials a nonsignificant positive deviation occurred (one-tailed $P = 0.22$). Hence, a period of covert prime-induced response competition preceded the overt execution of the correct response.

Covert prime processing could be observed even more directly.

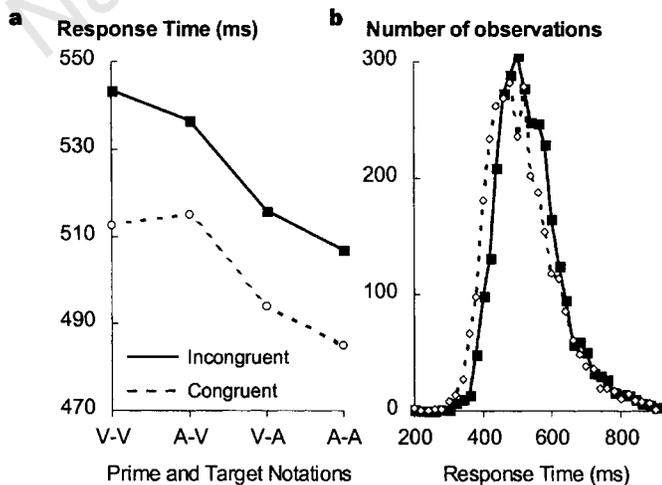


Figure 2 Behavioural priming effect. **a**, Average correct response times recorded during the ERP experiment are plotted as a function of prime–target congruity for different prime and target notations (A, Arabic; V, verbal). **b**, The distribution of correct responses showed a rightward shift in incongruent trials relative to congruent trials (bin size 20 ms).

Because the primes and targets were varied independently in the experimental list, we could test their impact on ERP recordings separately. Primes that induced a covert left-hand or right-hand bias produced a distinct pattern of brain activity over the left and right motor cortices (Fig. 4). Primes that were associated with the left hand during a given block caused a contralateral right-hemispheric negativity, and primes that were associated with the right hand caused a left-hemispheric negativity. This covert motor priming effect had a similar scalp topography to the overt motor effect that was found before the actual motor response to the target, but it was smaller and arrived earlier.

Because ERPs have a notoriously imprecise spatial resolution, we wanted to confirm that covert priming originated at least in part from motor circuits using the spatially accurate method of functional magnetic resonance imaging (fMRI). Response times recorded during fMRI recording replicated the prime–target congruity effect ($P = 0.0027$; effect size 20 ms). In fMRI, however, trials were now separated by 14 s, during which the rise and fall of the haemodynamic signal was measured in the whole brain every 2 s.

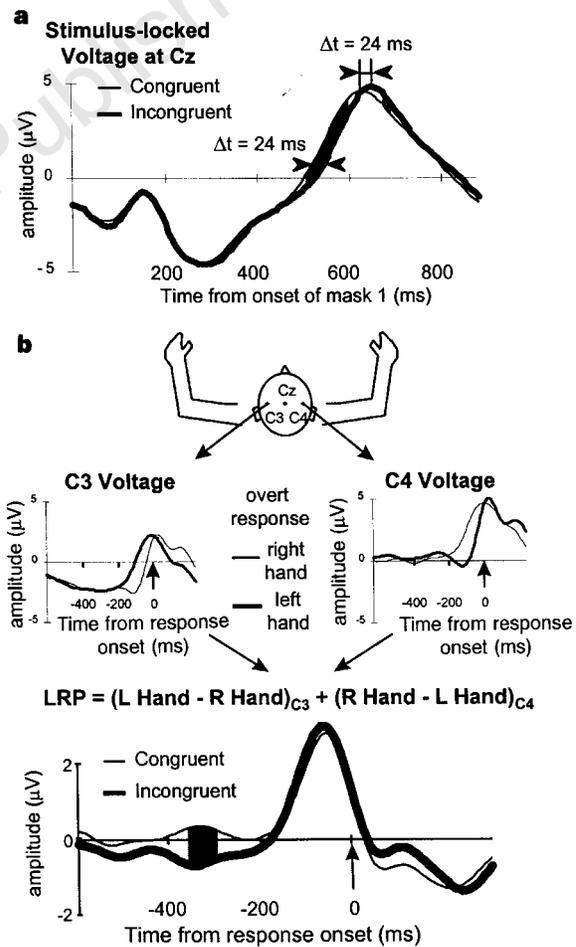


Figure 3 ERP measures of prime–target congruity. **a**, A late positivity (P3) recorded from the vertex from electrode Cz showed a significant delay in incongruent trials relative to congruent trials (shaded areas, $P < 0.05$). **b**, Derivation of the lateralized readiness potential (LRP). Individual trials were averaged in synchrony with the time of the key press, thus suppressing the effects of response delays. Electrodes C3 and C4 showed large voltage differences in opposite directions (top two graphs) before left-hand versus right-hand responses, reflecting the activation of the underlying motor circuits. The LRP (bottom) is the average of the differences at C3 and at C4, calculated according to the formula shown. In incongruent trials, before the main positive-going waveform reflecting overt response preparation, the LRP was significantly more negative than in congruent trials (shaded area, $P < 0.05$), reflecting covert motor priming.

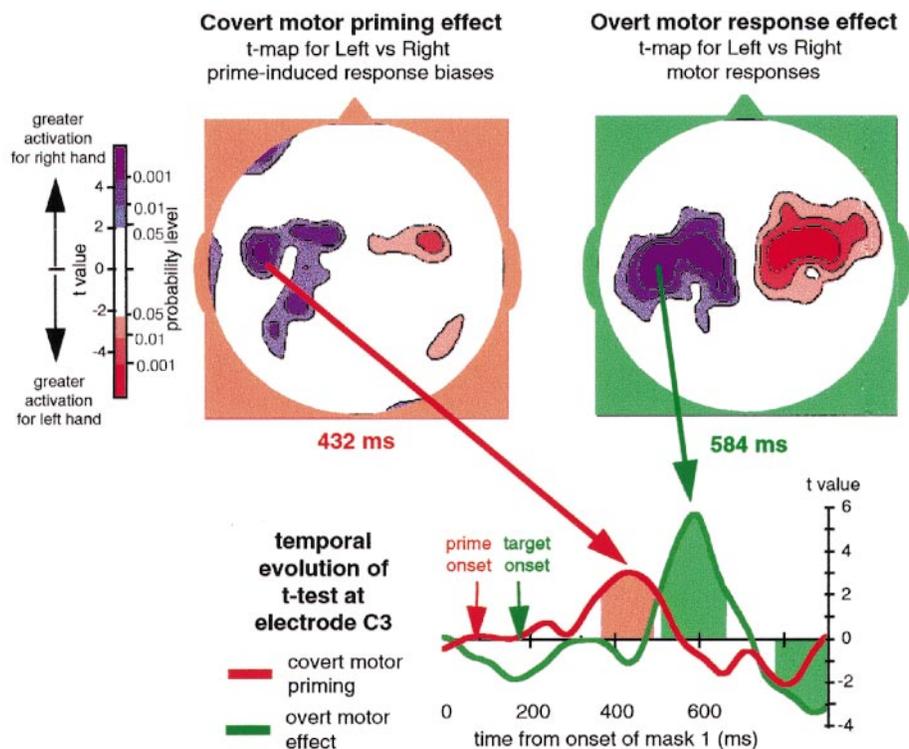


Figure 4 ERP measures of covert and overt motor activation. At each electrode site, two independent *t*-tests were performed on scalp voltages. The first test compared trials with overt target-induced right-hand or left-hand responses (green curve and top right map). The second test compared trials with primes inducing a covert left-hand or right-hand bias (orange curve and top left map). Statistical parameter maps in polar coordinates (top) show colour-coded *t*-test values at each site on the scalp, at the delay at which the effect was maximal. The

sign and topography of the covert motor priming effect and of the overt motor response effect are similar, indicating that primes and targets were processed in a similar way according to task instructions. The bottom curve shows the temporal evolution of the two independent *t*-tests at electrode site C3, positioned over the left motor cortex (coloured areas, $P < 0.05$). The covert effect preceded the overt effect by 162 ms, a delay roughly comparable to the interval between the onsets of the prime and target (114 ms).

Although this coarse haemodynamic measure cannot resolve the small activation delays associated with masked priming, we reasoned that it should be proportional to the total brain activity accumulated during a given trial, and should therefore reflect the sum of overt and covert activation in motor areas. We therefore extracted the fMRI signal profile from the left and right motor cortices, and used it to derive an index of lateralized motor activation analogous to the LRP, the lateralized bold response (LBR; Fig. 5). This measure showed a highly significant positive peak following each motor response. The LBR was smaller in incongruent trials than in congruent trials. The direction of this effect is identical to that seen in the LRP (Fig. 3b). Both effects indicate a significant prime-induced activation on the wrong response side on incongruent trials relative to congruent trials, diminishing the overall size of the activation on the correct motor side. Electrical and haemodynamic measures of covert masked priming were complementary: fMRI localized the priming effect to motor cortex, but was insensitive to its time course, whereas ERPs pinpointed the priming effect to a small window of time before the overt target-related motor activation.

Our results resolve the issue of the depth of processing of masked primes³. First, the results show that the processing of masked primes is accompanied by measurable modifications of electrical brain activity and of cerebral blood flow. This concurs with the observation of a modulation of amygdala activity by masked visual faces^{11,12}. As shown previously^{13,14}, brain imaging now has the potential to image unconscious cerebral processing. Second, unconscious activity is not confined to brain areas involved in sensory processing. Even areas involved in motor programming were covertly activated here, depending on the side of the motor response that subjects should have made if they had responded to the primes according to the task instructions. Because this motor parameter was determined by whether the prime was

larger or smaller than 5, the prime must have been categorized at the semantic level. By showing that a large amount of cerebral processing, including perception, semantic categorization and task execution, can be performed in the absence of consciousness, our results narrow down the search for its cerebral substrates. □

Methods

Procedure. All experiments were approved by the French ethical committee for biomedical research, and subjects gave informed consent. The stimulus set consisted of 64 pairs of prime and target numbers 1, 4, 6 and 9, each in either Arabic or spelled-out format. Subjects performed the number-comparison task twice in counterbalanced order. In one block, the instruction was to press the right-hand key for targets larger than 5 and the left-hand key for targets smaller than 5. In another block, the opposite instruction was used. Within each block, subjects received initial training (ERPs, 16 trials; fMRI, 25 trials) before the experimental session (ERPs, 256 trials; fMRI, 64 trials).

Event-related potentials. Twelve subjects were tested (six males; mean age 25; one other subject was rejected because of excessive motion). We presented a total of 512 stimuli at a 3-s rate on a standard PC-compatible SVGA screen (EGA mode, 70 Hz refresh rate). The electroencephalogram was digitized at 125 Hz from 128 scalp electrodes referenced to the vertex¹⁵, for a 2,048-ms period starting 400 ms before the onset of the first mask. We rejected trials with incorrect responses, voltages exceeding $\pm 100 \mu\text{V}$, transients exceeding $\pm 50 \mu\text{V}$, electro-oculogram activity exceeding $\pm 70 \mu\text{V}$, or response times outside a 250–1,000-ms interval. The remaining trials were averaged in synchrony either with stimulus or with response onset, digitally transformed to an average reference, band-pass filtered (0.5–20 Hz), and corrected for baseline over a 400-ms window before stimulus onset (similar results were observed with the raw, unfiltered data). Experimental conditions were compared by sample-by-sample *t*-tests on electrodes C3, C4 and Cz, with a criterion of $P < 0.05$ for five consecutive samples. Two-dimensional maps of scalp voltage and *t*-values were constructed by spherical spline interpolation¹⁶.

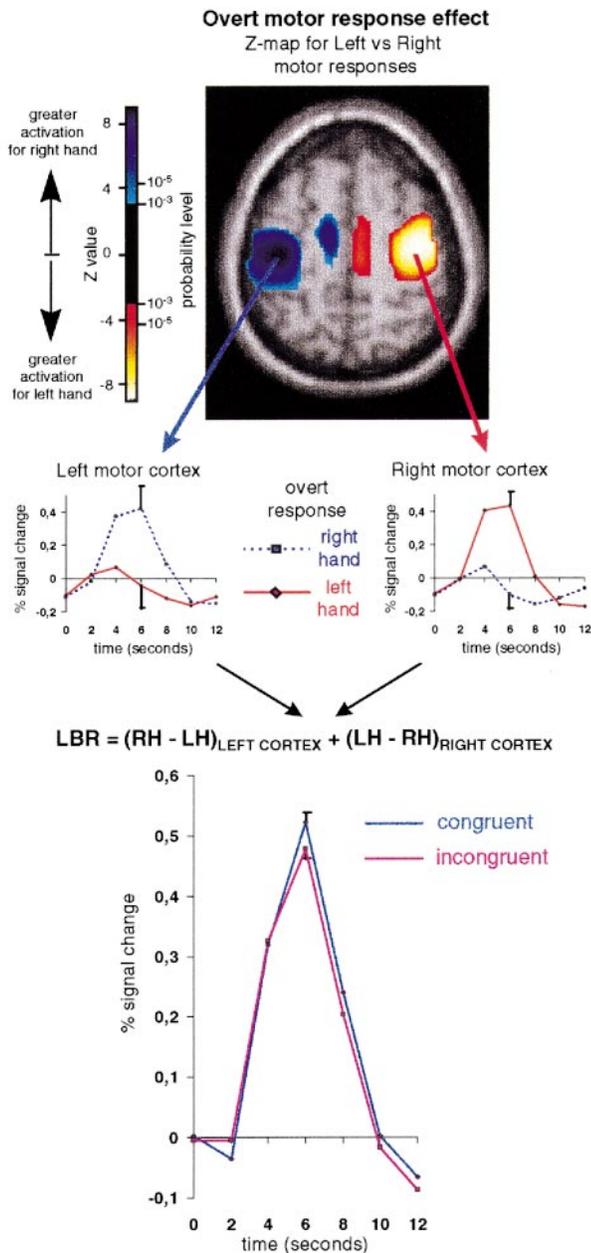


Figure 5 fMRI measure of motor priming. Top, voxels that showed significant differences in bold signal intensity between overt left-hand and right-hand responses are coded using the colour scale at left. The two voxels with the most significant overt motor effects were located in the left and right precentral cortex (Talairach coordinates $-39, -21, 66$ and $39, -15, 63$). Centre, plots of the average fMRI signal of the two voxels as a function of time show activation for contralateral movements following a haemodynamic delay of about 4–8 s (planned contrast for an increase in left–right differences from baseline (time points 0 and 2 s) to activated state (time points 4, 6 and 8 s): left motor cortex, $F(1, 8) = 20.1$, $P = 0.0021$; right motor cortex, $F(1, 8) = 27.0$, $P = 0.0001$). Bottom, it was therefore possible to construct an fMRI measure similar to the event-related LRP, indexing the time course of overt motor activation, which we term the lateralized bold response (LBR). The LBR was significantly larger (+9%) in congruent trials than in incongruent trials (interaction of the congruity factor with the baseline-to-activated-state contrast, $F(1, 8) = 6.23$, $P = 0.037$).

Functional magnetic resonance imaging. Nine new subjects were tested (seven males; mean age 26). We used an event-related design¹⁷. We presented a list of 128 randomly intermixed stimuli through mirror glasses and an active matrix video projector (EGA mode, 70 Hz refresh rate), with a 14-s inter-stimulus interval. In each trial, stimulus onset was synchronized with the

acquisition of the first slice in a series of seven volumes of eighteen slices each. We used a gradient-echo echo-planar imaging sequence sensitive to brain oxygen-level-dependent contrast (18 contiguous axial slices, 6-mm thickness, repetition time/echo time = 2,000/40 ms, in-plane resolution $3 \times 4 \text{ mm}^2$, 64×64 matrix) on a 3-Tesla whole-body system (Bruker). High-resolution anatomical images (three-dimensional gradient-echo inversion-recovery sequence, inversion time = 700 ms, repetition time = 1,600 ms, field of view = $192 \times 256 \text{ mm}^2$, matrix = $256 \times 128 \times 256$, slice thickness = 1 mm) were also acquired.

Analysis was done with SPM96 software. Images were corrected for subject motion, normalized to Talairach coordinates using a linear transform calculated on the anatomical images, smoothed (full-width at half-maximum = 15 mm), and averaged to define four types of event (congruent or incongruent \times left-hand or right-hand response). Images from all nine subjects were then analysed together. We used the generalized linear model to model the intensity level of each pixel as a linear combination, for each subject and each event type, of two activation functions with haemodynamic lags 4 and 7 s, thus allowing for differences in acquisition and activation times across slices and brain regions. We used a voxelwise significance level of 0.001, corrected to $P < 0.05$ for multiple comparisons across the brain volume.

Received 21 May; accepted 17 July 1998.

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Local control of information flow in segmental and ascending collaterals of single afferents

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In the vertebrate spinal cord, the activation of GABA(γ -aminobutyric acid)-releasing interneurons that synapse with intraspinal terminals of sensory fibres leading into the central nervous system (afferent fibres) produces primary afferent depolarization and presynaptic inhibition^{1–3}. It is not known to what extent these