process of jugal present; (9) exoccipital not fully fused with opisthotic; (10) lateral aperature for recessus scala tympani open; (11) interclavicle present; (12) ectepicondylar foramen present on humerus.

The primitive morphology of *S. hexatabularis* within the Amphisbaenia allows a reevaluation of the hypotheses of relationships of this group within the Squamata. Previous studies[11,14-16] have agreed that the sister group of the Amphisbaenia lies within the Scleroglossa, which includes all squamate families other than those of the Iguania[11]. Many of the studies suggest a close relationship between the Amphisbaenia and scincomorph lizards[11,17-20], but there has been no consensus. We propose a relationship within the scincomorpha between the Amphisbaenia and the Macrocephalosauridae[21] (part of the Polyglyphanodontinae[22]) on the basis of uniquely shared, derived features of the palate and temporal region (Fig. 3): the palatal ramus of the pterygoid is forked into a medial process, which extends along the medial side of the palatine and contacts or nearly reaches the vomer, and a lateral process which meets the ectopterygoid (sometimes the maxilla too) along the lateral side of the palatine and closes the suborbital fenestra (Fig. 2*b–g*); and a large postorbital is posteriorly broad, extends posteriorly over the temporal fenestrae, meets or closely approaches the parietal, and is excluded from the infratemporal fenestra by the contact of the jugal with the squamosal (Figs 2*j*, *k*; 4*a*). In addition, macrocephalosaurids occur in the same area of central Asia and the same geological period as *S. hexatabularis*.

Despite its well developed limbs and less specialized skull than that of later forms (Fig. 4*b–d*), the tiny supratemporal fenestra, heavily rugose dermal elements of the skull roof, solidly built cranium, posterolaterally facing orbit, large otic capsule with reduced occipital recess, and the massive stapes strongly suggest that *S. hexatabularis* was adapted to a fossorial way of life. □

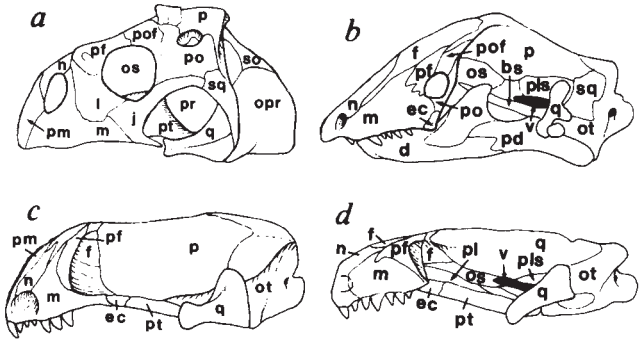

FIG. 4 Lateral views of four amphisbaenian skulls, showing a sequence of reductions of the supratemporal fenestral and orbit, and specializations of the skull for tunnelling. *a*, Reconstruction of holotype (IVPP V10593–1) of *Sineoamphisbaena hexatabularis*; *b*, a Middle Eocene amphisbaenian *Spathorhynchus fossorium*[3]; *c*, a living amphisbaenian *Bipes biporus* (the only living species with functional forelimbs), no. 145823, Museum of Comparative Zoology (MCZ); *d*, a living amphisbaenian *Amphisbaena alba*, no. 54299, MCZ. Illustrations are unscaled. Abbreviations as in previous figures, plus ot, fused otic/occipital complex; pd, fused postdentary complex; pls, pleurosphenoid (which is totally co-ossified with the prootic[8]). The skull of *S. hexatabularis* seems to be less specialized for tunnelling in soils when compared to those of later fossil and living species, which have an elongate, low skull with a spade-shaped or keeled snout. These differences may mean that *S. hexatabularis* lived in an environment very different from that of later fossil forms or living species. The Bayan Mandahu locality is thought to have been situated at the southern margin of an extensive sand sea dominated by eolian dunes[26]. This site is characterized by structureless eolian deposits with minor lacustrine and interdune fluvial deposits. *S. hexatabularis* may have tunnelled in the eolian deposits, using its limbs to dig tunnels and its broad heavily armoured interorbital skull table to ram-loose tunnel walls.

Received 28 April; accepted 25 August 1993.

1. Borsuk-Bialynicka, M. *Cretac. Res.* **12,** 607–608 (1991).
2. Astibia, H. *et al. Terra Res.* **2,** 460–466 (1991).
3. Berman, D. *Copeia* **4,** 704–721 (1973).
4. Gilmore, C. *Mem. natn. Acad. Sci.* **22,** 1–197 (1928).
5. Taylor, E. H. *Kans. Univ. Sci. Bull.* **34,** 521–579 (1951).
6. Berman, D. *J. Paleont.* **50,** 165–174 (1976).
7. Berman, D. J. *Paleont.* **51,** 986–991 (1977).
8. Zangerl, R. *Am. Midl. Nat.* **33,** 764–780 (1945).
9. Gans, C. *Bull. Am. Mus. Nat. Hist.* **119,** 129–204 (1960).
10. Gans, C. *Trans. zool. Soc. Lond.* **34,** 347–416 (1978).
11. Estes, R., Queiroz, K. & Gauthier, J. in *Phylogenetic Relationships of the Lizard Families* (eds Estes, R. & Pregill, G.) 120–280 (Stanford Univ. Press, California, 1988).
12. Rieppel, O. in *The Phylogeny and Classification of the Tetrapods* Vol. 1 (ed. Benton, M. J.) 261–294 (Clarendon, Oxford, 1988).
13. Jerzykiewicz, T. *et al. Can. J. Earth Sci.* (in the press).
14. Rage, J.-C. *Pour La Sci.* **1982,** 16–27 (1982).
15. Greer, A. E. *J. Herpetol.* **19(1),** 116–156 (1985).
16. Presch, W. in *Phylogenetic Relationships of the Lizard Families* (eds Estes, R. & Pregill, G.) 471–492 (Stanford Univ. Press, California, 1988).
17. Bogert, C. *Nat. Hist.* **73,** 17–24 (1964).
18. Rieppel, O. *J. Zool.* **195,** 493–528 (1981).
19. Böhme, W. in *Handbuch der Reptilien und Amphibien Europas* Vol. 1 (ed. Böhme, W.) 275–276 (Akademische Verlagsgesellschaft, Wiesbaden, 1981).
20. Schwenk, K. In *Phylogenetic Relationships of the Lizard Families* (eds Estes, R. & Pregill, G.) 569–598 (Stanford Univ. Press, California, 1988).
21. Suiminski, A. *Palaeont. pol.* **33,** 25–102 (1975).
22. Estes, R. *Handbuch der Paläoherpetologie* Vol. 10A (Fischer, Stuttgart, 1983).
23. Rieppel, O. *Zool. J. Linn. Soc.* **89,** 41–62 (1987).
24. Rage, J.-C. *Handbuch der Paläoherpetologie* Vol. 11 (Fischer, Stuttgart, 1984).
25. Bellairs, A.d'A. & Gans, C. *Nature,* **302,** 243–244 (1983).
26. Eberth, D. A. *Can. J. Earth Sci.* (in the press).

ACKNOWLEDGEMENTS. The specimens of *S. hexatabularis* were collected during the Dinosaur Project, an exchange between the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), the Canadian Museum of Nature, Ottawa, and the Royal Tyrrell Museum of Palaeontology (RTMP). They are housed in the IVPP. X.-C.W. thanks IVPP for allowing him to study the material and the RTMP for access to facilities. We thank D. A. Eberth for discussion, J. Rosado for the loan of skeletons of extant amphisbaenians, and C. Coy for photographing the type. X.-C. W. holds a University of Calgary postdoctoral fellowship; A.P.R. is supported by an NSERC operating grant.

An identified neuron mediates the unconditioned stimulus in associative olfactory learning in honeybees

Martin Hammer

Institut für Neurobiologie, Freie Universität Berlin, Königin-Luise Strasse 28/30, 14195 Berlin, Germany

DURING classical conditioning, animals learn to associate a neutral stimulus with a meaningful, or unconditioned, stimulus. The unconditioned stimulus is essential for forming associations, and modifications in the processing of the unconditioned stimulus are thought to underlie more complex learning forms[1–4]. Information on the neuronal representation of the unconditioned stimulus is therefore required for understanding both basic and higher-order features of conditioning. In honeybees, conditioning of the proboscis extension reflex occurs after a single pairing of an odour (conditioned stimulus) with food (unconditioned stimulus)[5,6] and shows several higher-order features of conditioning[6–8]. I report here the identification of an interneuron that mediates the unconditioned stimulus in this associative learning. Its physiology is also compatible with a function in complex forms of associative learning. This neuron provides the first direct access to the cellular mechanisms underlying the reinforcing properties of the unconditioned stimulus pathway.

Neurons mediating the reinforcing property of the unconditioned stimulus (US) in conditioning must meet two criteria: response to the US and convergence with the conditioned stimulus (CS) pathway. To identify such neurons in conditioning of the proboscis extension reflex, an *in vivo* preparation was developed in which single cells in the suboesophageal ganglion were impaled, tested for their responsiveness to the US (sucrose solu-

tion applied briefly to the antennae and proboscis), and subsequently stained with Lucifer yellow. One particular candidate neuron, VUMmx1, was identified by its specific response characteristics and unique morphology (Fig. 1). It responds to sucrose with a long burst of action potentials (duration ~30 s; frequency over 30 s, 4.6 ± 0.5 Hz (mean, s.e.m.); $n = 10$) which outlasts the US. VUMmx1 arborizes in the dorsal suboesophageal ganglion and innervates brain neuropiles involved in odour (CS) processing: that is, the antennal lobe glomeruli, the lateral protocerebrum and the mushroom body calyces[9,10]. It therefore shows multiple convergence onto CS-processing neuropiles.

As an appetitive stimulus, the US has several properties. It releases behavioural acts, such as the proboscis extension reflex, transiently sensitizes feeding behaviour (non-associative modulations)[11], and serves as a reinforcer in conditioning. As these properties may be processed in parallel at the neural level, all neurons responding to sucrose do not necessarily mediate conditioning. To investigate whether VUMmx1 meets a third essential criterion for mediating reinforcement in learning, bees were conditioned to an odour in a single trial, in which sucrose as a US was replaced by a supra-threshold depolarization of VUMmx1 (Fig. 2*a*).

Bees only learn to respond to an odour with the proboscis extension reflex (conditioned response) when it is presented shortly before the US during conditioning[5] (Fig. 2*c*, open bars); that is, associative learning depends on temporal contiguity between CS and US. Thus, by presenting an odour either before (forward pairing; $n = 12$) or after (backward pairing; $n = 11$) the start of depolarizing VUMmx1 (Fig. 2*a*), associative effects could be discriminated from non-associative effects. Odour responses were quantified by comparing odour-evoked electromyograms from muscle M17, which controls the proboscis extension reflex[12], in 10-s intervals after odour onset 5 min before (pre-test) and 10 min after (test) pairing (Fig. 2*b*). For forward pairing, the number of M17 spikes increased from pre-test to test (Fig. 2*c*) (pre-test, 1.5 (0,11); test, 61 (28,101.5); median of spikes (interquartile ranges); $P < 0.05$). Occasionally M17 activity increased during forward pairing (median: 42.5 (1.5,61.5) spikes, NS), which might indicate that coincidence of an odour and VUMmx1 activity immediately alters odour processing. VUMmx1 probably does not directly contribute to PER, however, because its depolarization does not evoke motor activity during backward pairing. Furthermore, the backward pairing group reveals that replacing a sucrose reward by depolarizing

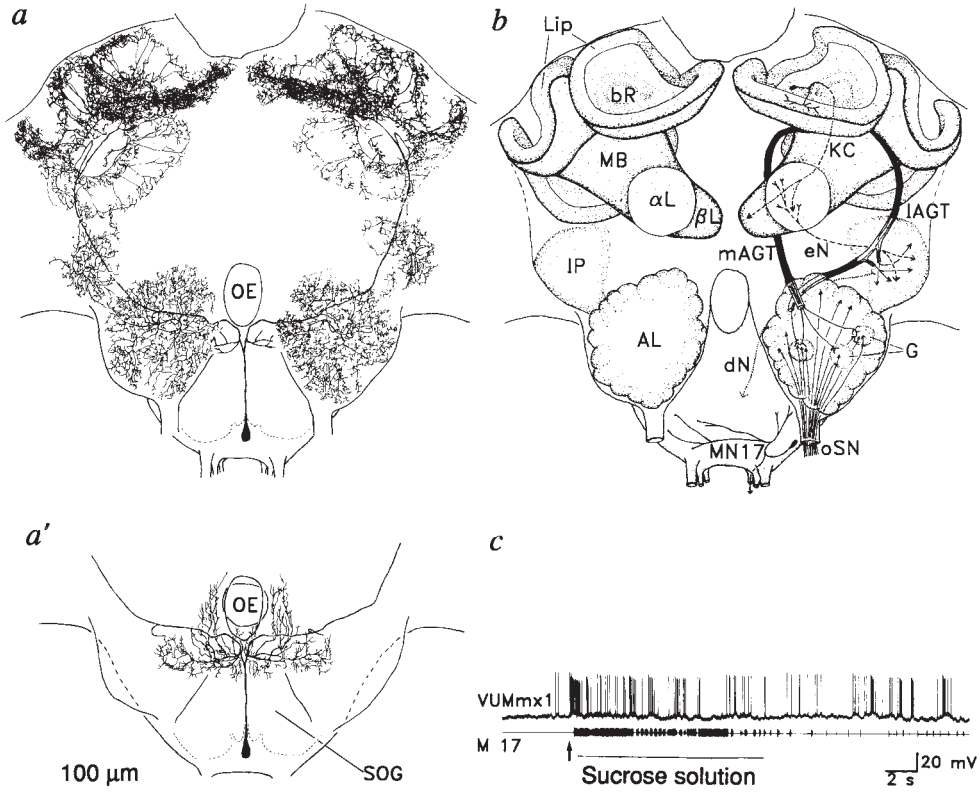

FIG. 1 Morphology of VUMmx1 (ventral unpaired median cell of maxillary neuromere 1) and its response to sucrose (US). *a* and *a'*, Morphology: *a*, VUMmx1 innervates the glomeruli (G in *b*) of the antennal lobes (AL), the lateral protocerebrum (IP), and lips and basal rings (bR) of the mushroom bodies (MBs) calyces (for orientation, see *b*); *a'*, in the suboesophageal ganglion (SOG) the primary neurite projects dorsally from the ventral median soma and bifurcates beyond the oesophagus (OE). Dendritic arborizations occur in the dorsal SOG and the tritocerebrum. VUMmx1 is one of a group of VUM neurons in the maxillary neuromere, but can be reliably identified by its unique morphology. *b*, Scheme of the olfactory pathway. Olfactory sensory neurons (oSN) from the antennae serve the glomeruli. Relay neurons connect glomeruli with the IP and the calyces via two fibre tracts (lAGT and mAGT)[9,10]. In bees, the MBs calyces receive various modalities separately: the lip primarily olfactory, the collar visual, and the basal ring multimodal, thought to arise partly from collaterals of visual and olfactory fibres[10]. Kenyon cells (KC) distribute information to the MBs output lobes (αL and βL). Some extrinsic neurons (eN) connect the MB with the IP[24]. Motor neurons (such as MN17) generating the proboscis extension reflex (PER) are located in the ventral SOG[25]. In insects, descending neurons (dN) are thought to connect the IP with motor centres[26]. c, Long-lasting excitation of VUMmx1 following application of sucrose to the antennae and proboscis (arrow). Little, if any, phasic excitation is elicited by visual and mechanical stimuli to the mouthparts and antennae. Lower trace: corresponding PER recorded as an electromyogram from M17.
METHODS. Bees were fixed by waxing the dorsal thorax to a small metal table, which allowed free movements of mouth parts and antennae. Impaled neurons were stained with Lucifer yellow (5%; hyperpolarizing current pulses, 2–8 nA, for 10–40 min). As in conditioning experiments, sucrose solution (~30%) was briefly (<1 s) delivered to the antennae and proboscis. Odours (carnation) were presented in a gentle air stream. Stimulus duration was controlled with a solenoid valve.

VUMmx1 during conditioning alters CS processing in a way that is dependent only on a specific associative feature: temporal contiguity between the CS and VUMmx1 activity. The test response after forward pairing depends on the temporal relations during pairing as it significantly exceeds that after backward pairing (Fig. 2*c*) ($P<0.002$). This difference cannot be due to a different spike frequency of VUMmx1 during depolarization (forward, 7.8 ± 0.7 Hz; backward, 7.9 ± 0.7 Hz).

Using sucrose as the US under the same experimental conditions, without intracellular recording, the response to an odour after forward pairing (median: 70(21,135) M17 spikes; $n=15$; Fig. 2*c*) was no different from that recorded in substitution experiments. Thus, VUMmx1 is an equally effective US as is sucrose. But as VUMmx1's spike frequency in substitution experiments exceeds its sucrose response, other neurons may also be involved in mediating the US.

The observation that odours elicit a short phasic excitation of VUMmx1 (Figs 2*b*, 3*a*) raises the possibility that the efficacy of the olfactory input to VUMmx1 is altered after pairing. Quantitative analysis of VUMmx1's odour response (Fig. 3) reveals an increase in the total number of VUMmx1 spikes from 12.1 ± 2.5 (pre-test) to 26.0 ± 6.4 spikes (test) for forward ($P<0.025$) but not backward pairing (pre-test, 11.7 ± 2.5; test, 9.2 ± 1.7; $P<0.05$ between tests after forward and backward pairing). An analysis of the spike frequency in 15 consecutive 1-s intervals indicates that the increased response after forward pairing is due to a long-lasting excitation (Fig. 3*b*). Temporal coincidence of activity in the olfactory system and VUMmx1

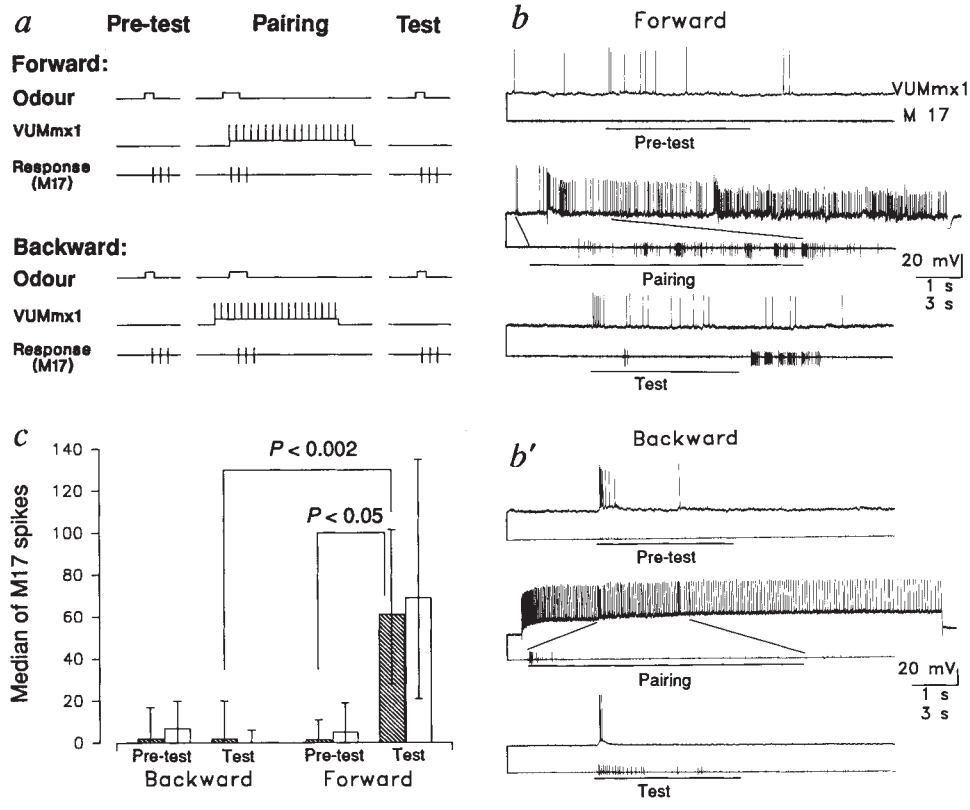

FIG. 2 Substitution of VUMmx1–depolarization for the US in PER conditioning increases subsequent odour responses of bees when the temporal relations between odour stimulus and VUMmx1 activity are correct. *a*, Experimental design. During pairing, an odour (duration, 6 s) is delivered in temporal proximity with spike activity of VUMmx1 evoked by current injection (duration, 30 s). In forward pairing, odour onset precedes depolarization by 2 s; in backward pairing, it follows 5 s after onset of depolarization. Effects of treatment are recorded as electromyograms (EMGs) from M17 by comparing odour responses 5 min before (pre-test, stimulus duration 3 s) and 10 min after pairing (test, duration 3 s). *b* and *b'*, Response change induced by depolarizing VUMmx1. Intracellular recordings from VUMmx1 (upper traces) and EMGs from M17 (lower traces) before, during and after substitution of a sucrose reward by depolarizing VUMmx1. VUMmx1 depolarization is shown on a slower timescale. (Calibration scale: lower time value, upper of middle two traces only; upper value, all other traces.) In *b*, an example is shown of a forward pairing of odour and depolarization (recording trace during depolarization is displayed a.c.-coupled); *b'* shows an example of a backward pairing. *c*, Quantitative comparison of the effect of the substitution experiment (hatched bars; $n=11$ for backward, $n=12$ for forward). Data are shown for comparison from a parallel group of control bees (without intracellular recording) trained with either forward or backward pairing, in which sucrose was used as US (open bars, $n=15$ for each group). Data are expressed as median (with interquartile ranges) number of M17 spikes in a 10-s interval after odour onset.

METHODS. Timing between CS and VUMmx1 depolarization was adjusted according to behavioural studies[5]. Test odours were presented 10 min after pairing, because retrieval in PER conditioning is exclusively controlled by an associative memory ~7 min after a single learning trial[6,11]. Depolarization current of 0.8–1.6 nA was injected to evoke spike activity of VUMmx1. As sufficient balancing of the microelectrode resistance was not always possible, recordings were stored d.c.- and a.c.-coupled. Impaled cells were identified as VUMmx1 by staining with Lucifer yellow. Bees were stimulated with sucrose at 3–5 min after test to ensure that the failure of the backward-paired bees to show PER was not due to performance impairment (median of M17 spikes: forward, 315 (264,387); backward, 301 (252,430)). Four bees per group showing no or an impaired PER were excluded from analysis. Non-parametric statistics for independent (*U*-test) or correlated data sets (Wilcoxon test), respectively, were used for data sets with cutoffs or without normal distribution. Appropriate parametric statistics were applied in all other cases (*t*-test, paired *t*-test). Two-tailed statistics were used throughout.

thus induces an increase of the olfactory input to VUMmx1 which may depend on the associative strength of odours. Monitoring VUMmx1's activity during differential conditioning supports this hypothesis (Fig. 4). Differentially conditioned bees associate one odour (CS^+) specifically paired with the US as an indicator for food, but do not associate another specifically unpaired odour (CS^-)[7]. After successful differential conditioning, VUMmx1's response to the CS^+ increases compared with pre-test (Fig. 4*b*; pre-test, 11.4 ± 3.9; test, 41.3 ± 10.6 spikes; $P < 0.015$; $n = 5$). This difference is pairing-specific. The test response to the CS^+ significantly exceeds that to the CS^- (7.8 ± 4.0; $P < 0.03$). VUMmx1 responds to the CS^+ with a prolonged excitation (Fig. 4*b*). Thus, VUMmx1 has a discharge to a learned odour similar to that produced by the US (Fig. 1*c*).

Tracing modulatory or reinforcing pathways has helped to validate ideas about cellular mechanisms of plasticity and to scrutinize sites of plasticity in non-associative[13] and associative learning models[14,15]. My study provides evidence that a single neuron is sufficient to mediate reinforcement in associative learning. But the difference in the strength of VUMmx1's sucrose response and the depolarization effective in substitution experiments suggests that other neurons participate in mediating the US. A serial homologue of VUMmx1, for example, has an almost identical branching pattern and also responds to sucrose. Correlating VUMmx1 activity in substitution and conditioning experiments, in which sucrose is used as US, with learning success should provide evidence for this interpretation

The distribution of branches of VUMmx1 indicates crucial brain structures for associative learning. VUMmx1 converges with the CS pathway in three different brain regions, reinforcing the concept that integration underlying learning and memory occurs at multiple sites. This and other studies in bees[16,17] and fruitflies[18-21] implicate the mushroom bodies in such higher brain functions. The restriction of VUMmx1's branches in the mushroom bodies to the calyces is the first indication that memory induction occurs at the mushroom body input sites. VUMmx1's projections in the antennal lobes and lateral protocerebrum, however, emphasize that these structures may also be involved in associative learning.

VUMmx1 fails to evoke motor activity during backward pairing, indicating parallel processing of reflex and reinforcement. This could allow the uncoupling of reflexive behaviour from alterations in the effectiveness of the reinforcing pathway, which may underlie more complex forms of learning. The plasticity of VUMmx1's odour response suggests its involvement in processing higher-order features of conditioning. After forward pairing, the odour elicits a long-lasting discharge of VUMmx1, indicating that its responsiveness to an odour could depend on the associative strength of that odour. The difference of VUMmx1's odour response to two differentially conditioned odours confirms this hypothesis. Learning therefore adds more to a CS than the capacity to evoke a conditioned response: a learned CS also activates VUMmx1. VUMmx1 can thus maintain its functional property of mediating the reinforcer in the absence of the US, a feature that could underlie second-order conditioning, for instance[4,22,23]. □

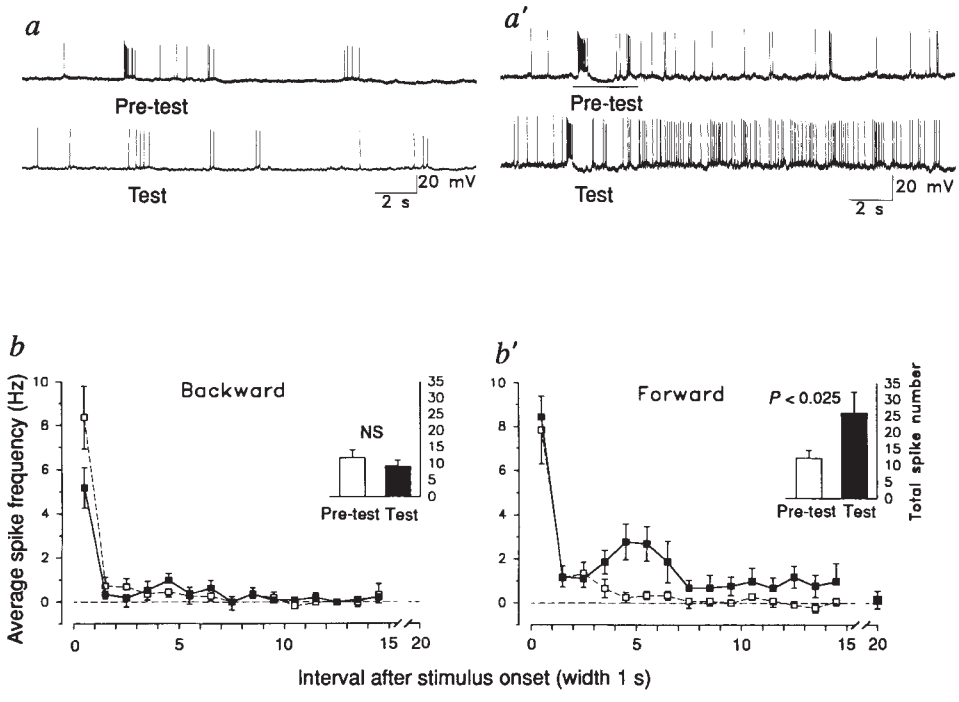

FIG. 3 Plasticity of VUMmx1's odour response in substitution experiments. *a* and *a'*, The phasic odour response is reduced after backward pairing in the test compared with pre-test (*a*) but is increased after forward pairing to a long-lasting excitation (*a'*). *b* and *b'*, Post-stimulus interval histogram from 15 consecutive 1-s intervals after stimulus onset. The spike frequency (mean, s.e.m.) in each interval is calculated as the number of spikes in that interval minus the spontaneous frequency 10 s before stimulus onset. Baseline activity is shown as a dashed line at 0 Hz. The excitation of VUMmx1 in the forward paradigm drops to baseline during interval 16 to 20 (large black square in *b'*). The total number of spikes (spike number minus baseline) in 15 s after stimulus onset increases after forward pairing for the test compared with pre-test, but is unchanged following backward-pairing (see insets).

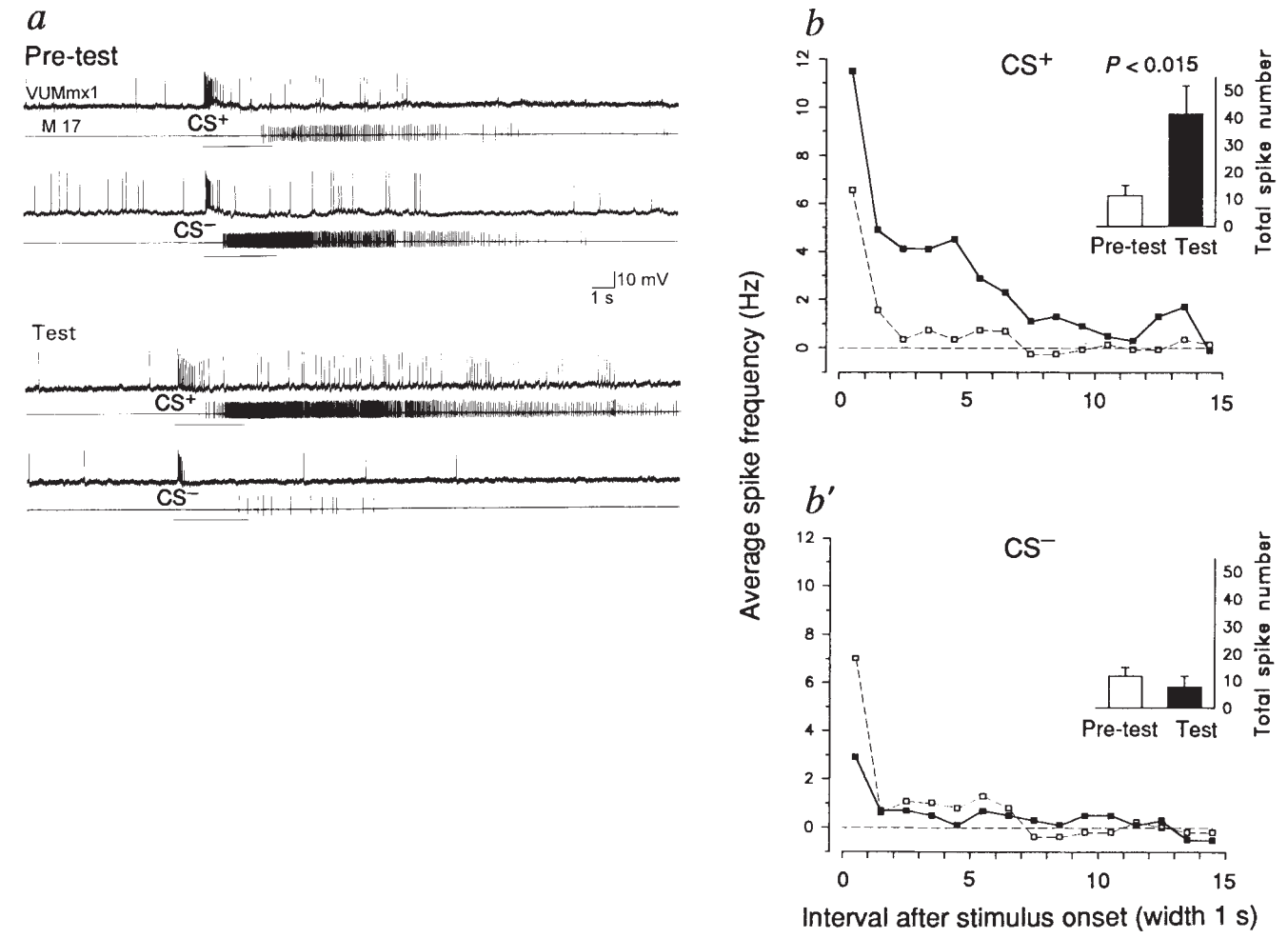

FIG. 4 Response plasticity of VUMmx1 in differential conditioning experiments ($n=5$). Bees were differentially conditioned to two odours (carnation or orange-blossom) in 5 trials. One odour was specifically paired with the US (CS^+; intertrial interval, 1 min). The other (CS^-) was delivered specifically unpaired inbetween. Selection of odours as CS^+ or CS^- was exchanged in consecutive experiments. *a*, Responses recorded from VUMmx1 and M17 5 min before (pre-test) and 10 min after (test) differential conditioning. A spontaneous PER to both odours is evoked during pre-test, as indicated by EMGs. Test responses of VUMmx1 and M17 to CS^+ are increased in strength and duration, whereas responses to CS^- are decreased (M17) or remain unchanged (VUMmx1). *b* and *b′*, Post-stimulus interval histogram reveals that the significant increase in VUMmx1's response to the CS^+ in the test as compared with pre-test (inset) is due to a prolonged excitation (*b*). The small drop in the total spike number for the CS^- (inset) is due to a reduction of the phasic excitation of VUMmxl (*b′*). A second test (5–10 min after the test), with reversed order of odours to exclude extinction-like effects between successive odour stimulations, reveals the same results. Spike numbers were calculated as for Fig. 3.

Received 16 April; accepted 13 September 1993.

1. Rescorla, R. A. *A. Rev. Neurosci.* **11,** 329–352 (1988).
2. Rescorla, R. A. & Wagner, A. R. in *Classical Conditioning II: Current Research and Theory* (eds Black, A. H. & Prokasy, W. F.) 64–99 (Appleton–Century–Crofts, New York, 1972).
3. Wagner, A. R. in *Information Processing in Animals: Memory Mechanisms* (eds Spear, N. E. & Miller, R. R.) 5–47 (Erlbaum, Hillsdale, N J, 1981).
4. Hawkins, R. D. & Kandel, E. R. *Psychol. Rev.* **91,** 375–391 (1984).
5. Menzel, R. & Bitterman, M. E. in *Neuroethology and Behavioral Physiology* (eds Huber, F. & Markel, H.) 206–215 (Springer, Berlin, 1988).
6. Menzel, R. in *Neurobiology of Comparative Cognition* (eds Kesner, R. P. & Olton, D. S.) 237–292 (Erlbaum, Hillsdale, NJ, 1990).
7. Bitterman, M. E., Menzel, R., Fietz, A. & Schäfer, S. *J. comp. Physiol.* A**97,** 107–119 (1983).
8. Smith, B. H. *J. exp. Biol.* **161,** 367–382 (1991).
9. Arnold, G., Masson, C. & Budharugsa, S. *Cell Tissue Res.* **242,** 593–605 (1985).
10. Mobbs, P. *Phil. Trans. R. Soc.* B**298,** 309–354 (1982).
11. Menzel, R., Greggers, U. & Hammer, M. in *Insect Learning: Ecological and Evolutionary Perceptives* (eds Papaj, D. R. & Lewis, A. C.) 79–125 (Chapman & Hall, New York, London, 1993).
12. Rehder, V. *J. Insect Physiol.* **33,** 303–311 (1987).
13. Mackey, S. L., Kandel, E. R. & Hawkins, R. D. *J. Neurosci.* **9,** 4227–4235 (1989).
14. Mauk, M. D., Steinmetz, J. E. & Thompson, R. F. *Proc. natn. Acad. Sci. USA.* **83,** 5349–5353 (1986).
15. Farley, J. *Behavl Neurosci.* **101,** 28–56 (1987).
16. Erber, J., Mazur, T. & Menzel, R. *Physiol. Entomol.* **5,** 343–358 (1980).
17. Mauelshagen, J. *J. Neurophysiol.* **69,** 609–625 (1993).
18. Heisenberg, M., Borst, A., Wagner, S. & Byers, D. *J. Neurogenet.* **2,** 1–30 (1985).
19. Balling, A., Technau, G. M. & Heisenberg, M. *J. Neurogenet.* **4,** 65–73 (1987).
20. Nighorn, A., Healy, M. J. & Davis, R. L. *Neuron* **6,** 455–467 (1991).
21. Han, P.-L., Levin, L. R., Reed, R. R. & Davis, R. L. *Neuron* **9,** 619–627 (1992).
22. Buonomano, D. V., Baxter, D. A. & Byrne, J. H. *Neural Networks* **3,** 507–523 (1990).
23. Hawkins, R. D. in *Computational Models of Learning in Simple Neural Systems* (eds Hawkins, R. D. & Bower, G. H.) 65–108 (Academic, San Diego, 1989).
24. Rybak, J. & Menzel, R. *J. comp. Neurol.*, **334,** 444–465 (1993).
25. Rehder, V. *J. comp. Neurol.* **279,** 499–513 (1989).
26. Strausfeld, N. *Atlas of an Insect Brain* (Springer, Berlin, Heidelberg, New York, 1976).

ACKNOWLEDGEMENTS. I thank R. Menzel for support and encouragement, and R. Menzel and especially P. Stevenson for their comments on the manuscript.