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Robust judgement of inter-object distance by an arthropod

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Animals use several strategies for depth vision, reflecting the constraints imposed by body size, the structure of the visual system and the visual geometry of the environment¹. Arthropods in particular have restricted depth perception, because they are small and possess closely set, low-resolution compound eyes. Yet, here we show that fiddler crabs defending their burrows from conspecifics can judge how close other crabs are to their burrow. When confronted with small dummy crabs, the burrow owners assess the dummy's position and motion relative to their burrow and not relative to themselves—in other words, by using an allocentric rather than an egocentric frame of reference. Irrespective of their own distance from the dummy, the likelihood that the crabs rush back to defend their burrow increases strongly as the dummy approaches the burrow. In addition, the mean dummy–burrow distance at which the crabs respond is constant and independent of the dummy's direction of approach. We propose that to solve this sophisticated task of relative distance judgement, the crabs combine visual information on dummy position and direction with information on burrow location acquired during path integration². In doing so, the crabs, like humans³, make clever use of the visual geometry of their environment.

The fiddler crab *Uca vomeris* lives in dense colonies on tropical and subtropical mud and sandflats, commonly with between 10 and 20 animals per square metre. Each individual operates from its own burrow, which it defends vigorously against other crabs^{4–7}. Burrow

defence is not a trivial task because in most cases foraging crabs cannot see the entrance to their burrow owing to perspective foreshortening⁸. To determine how fiddler crabs detect and assess conspecifics approaching their burrows, we moved small dummy crabs across the ground towards a burrow while the burrow owner was away feeding. We subsequently reconstructed from video tapes the exact spatial constellation of the dummy, the crab and its burrow in a frame-by-frame analysis to determine the timing of burrow-defence responses and the visual cues triggering them.

When confronted with a dummy crab approaching their burrow, burrow owners respond by dashing back to their burrows, just as they would in response to real crab intruders. Figure 1 documents two such burrow-defence responses. In the first scene (Fig. 1a), the crab slowly retreats to its burrow once the dummy has approached to within 21 cm of the entrance. The crab then remains close to the burrow until the dummy has left. In the second scene (Fig. 1b), the same crab is on the other side of the burrow when the dummy approaches and responds when the dummy has reached a similar dummy–burrow distance (26 cm), even though the crab–dummy distance at this point is still much larger than in the first scene (Fig. 1a). The crab responds with a fast home run that takes it all the way back to the burrow. After the dummy has reached its closest approach, the crab begins to move away from the burrow. But as soon as the dummy returns from the end of its track, the crab rushes home for the second time, where it remains until the dummy has moved out of the area.

We find that the response probability increases strongly as the dummy approaches the burrow (Fig. 2, black line), resulting in a cumulative response probability that reaches 66% at 10 cm (Fig. 2, grey line). As there is no defined dummy–burrow distance for trials in which the crabs did not react, we used the variable 'track distance', which measures the closest distance between the dummy track and the crab's burrow (see Fig. 3a) and varied between 5 and 55 cm, to test for the effect of the dummy–burrow distance on the crab's response probability. Statistical analysis shows that the track distance is the main factor that determines whether a crab responds to these dummies or not ($P < 0.001$). The probability of response decreases from over 80% for track distances of 5–10 cm, to below 20% for track distances of more than 50 cm.

The crabs tend to stay close to their burrows and the track distance is therefore correlated with the distance between the crab and the dummy track. To ensure that response probability is indeed determined by the dummy–burrow distance and not by the crab–dummy distance, we removed the (burrow) track distance from the

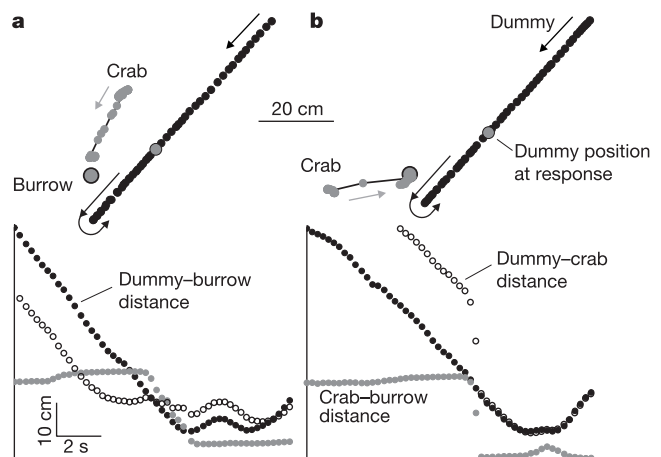


Figure 1 Two examples of a fiddler crab (*Uca vomeris*) responding with burrow defence to an approaching crab dummy. The top section of each panel shows the dummy, the crab and the burrow from above. Dots mark the dummy and crab positions at 240-ms intervals.

model and fitted the crab–track distance instead. Again, we could not use crab–dummy distance directly because it is not defined for trials in which crabs did not react. The crab–track distance has no explanatory power (generalized linear mixed model (GLMM): degrees of freedom (d.f.) = 1, Wald/d.f. = 0.37, $P = 0.543$), even when we allow for a difference in response depending on whether the dummy approaches from the crab's side of the burrow or not (GLMM: d.f. = 1, Wald/d.f. = 0.29, $P = 0.748$). The effects of additional variables in the statistical model are summarized in Methods. The distance between the dummy and the burrow is thus the most important predictor of whether a crab reacts or not.

We examined what determines the timing of the response by investigating the parameters that affect the response distance, which is the dummy–burrow distance at the moment the crabs decide to respond. Statistical analysis showed that the average response distance was 23.8 cm and was unexpectedly constant across many factors (see Methods and Fig. 3a). Most notably, the crabs react at almost equal dummy–burrow distances, irrespective of the dummy's approach direction and consequently of the distance between crab and dummy (Fig. 3b). The statistical model identifies a small influence of the dummy's direction of approach (track angle), which just reaches significance ($P = 0.028$). But this effect is very small and is caused by the crabs reacting slightly late whenever the dummy approaches from beyond the burrow (Fig. 3b).

Whereas the crabs keep the response distance constant, irrespective of the dummy's approach direction, they are able to adjust the response distance (dummy–burrow distance) according to their own distance from the burrow. For small track distances, there is a positive effect of the crab–burrow distance on the response distance. The further away the crabs are from the burrow, the earlier they respond to the dummy ($P < 0.001$). The crabs thus know their own distance from the burrow, most probably through path integration². The main conclusion from these results is that fiddler crabs can measure the distance between a dummy crab and their burrow, irrespective of the relative angle under which they view the dummy and the burrow.

Are the crabs also sensitive to the movement direction of the dummies? To investigate this possibility, we selected all experiments in which the dummy moved at least 5 cm past the closest point to the burrow before changing direction at the return point, including experiments where the crabs did not react at all or reacted late after the dummy had moved past the closest point (Fig. 4, inset). If the crabs discriminate between approaching and retreating dummies, then we expect the response probability to be higher for segments 1 and 3 than for segments 2 and 4.

The data in Fig. 4 clearly show that the crabs distinguish between approaching and retreating dummies. The response probability is significantly higher for track segments 1 and 3 than for segments 2 and 4 (GLMM: d.f. = 3, Wald/d.f. = 11.95, $P < 0.001$). On the basis of the pair-wise standard errors of the linear transformation of the model, all four segments are significantly different from each

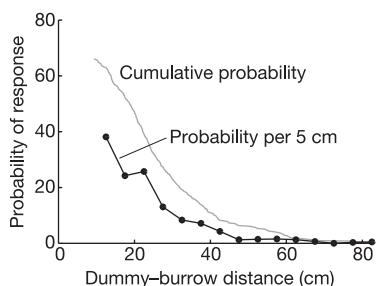


Figure 2 The crabs' response probability (%) depends on the dummy–burrow distance. The black unbroken line shows the probability that the crabs react in a 5-cm interval. The grey line shows the corresponding cumulative response probability.

other. Because the dummies always moved through the segments in the order 1 to 4, one might expect the response to decline towards later segments, because the more sensitive crabs might react earlier in the sequence. The most important comparison is therefore between segments 2 and 3, which clearly confirms the hypothesis that the crabs are sensitive to the dummy's direction of motion. In addition, the response probability is higher in segment 3 than in segment 1, which suggests that the crabs are sensitized by the change of the dummy's direction at the return point.

We suggest that the onset of burrow defence in fiddler crabs depends on two variables: the distance of an intruder to the owner's burrow; and the intruder's direction of motion relative to the burrow—that is, whether the intruder approaches it or not. Fiddler crabs are thus able to assess the distance and the motion direction of other crabs not only in an egocentric frame of reference, but also relative to a distant, invisible location in the world, in other words, a geocentric frame of reference.

The predictable visual geometry of the flat world fiddler crabs inhabit allows them to use a simple solution for what seems to be the complex geometrical problem of judging the distance between two objects independently of the viewing angle and distance. Theoretically, in the crabs' visual environment the distance of objects on the ground can be determined by retinal position (elevation) alone^{1,3,9}. The crabs carry their eyes at a constant height above ground on long, vertical eye stalks, and when foraging away from the burrow they

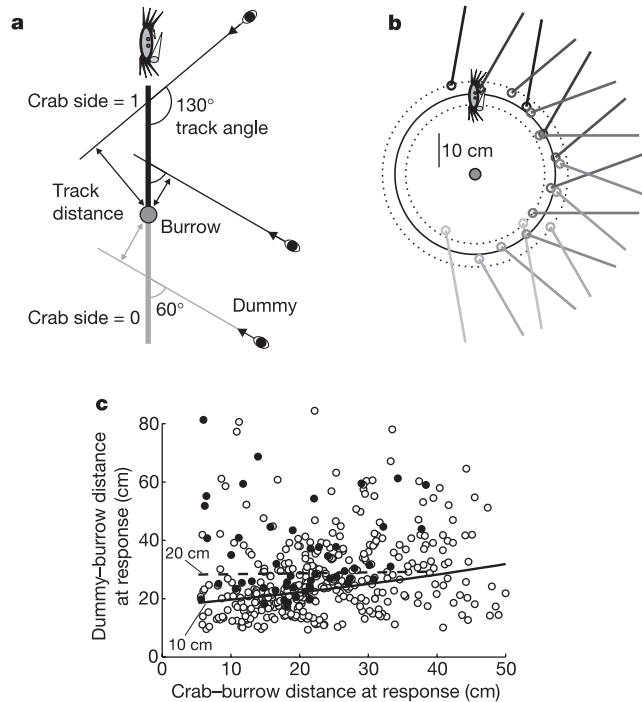


Figure 3 The timing of the burrow defence response. **a**, Definition of parameters. The approach direction (track angle) was fitted as a factor with nine directions (20° bins). **b**, The dummy–burrow distance at the time of the response is constant. The solid lines show the dummy's trajectory and the large dots mark its position at the time of the response as fitted by the statistical model. The response distance is shown for each of the nine approach directions (track angle) and the two values of crab side. Increasing track angles are shown in progressively lighter greys. The unbroken and dotted circles represent the mean reaction distance and ± 2 s.e.m., respectively. Fitted values were calculated at the mean of all other parameters in the statistical model (crab–burrow distance = 23.4 cm). **c**, For small track angles, the crabs adjust the response distance according to their own distance from the burrow (open circles, track distance < 15 cm; filled circles, track distance ≥ 15 cm). The corresponding model fit is shown as an unbroken line for a track distance of 10 cm and as a dashed line for a track distance of 20 cm.

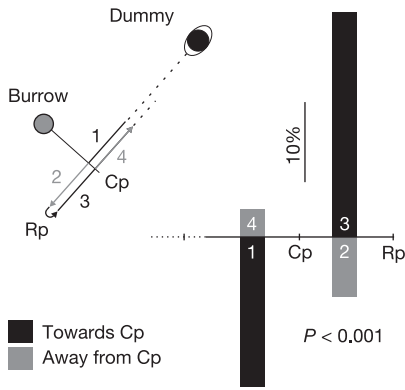


Figure 4 The probability of response for four length-matched segments around the closest point (Cp) of the dummy track to the crab's burrow (see inset). Only the first response of a crab was counted. If a crab responded in a given segment, then its response during the remainder of the sequence was ignored. Experiments in which the crabs reacted before the dummy reached segment 1 were not included. The number of trials contributing to segments were 232, 176, 162 and 123, respectively. Rp, the return point of the dummy at the end of the track.

keep their longitudinal body axis aligned with the home vector². The burrow environment is thus always viewed by the lateral retina. For a given crab–burrow distance, the crabs' ability to measure the distance between an object and the burrow could thus be based on a single, wide-field, motion-sensitive neuron (distance neuron) with a gradient of sensitivity to small objects that increases towards the retinal position of the burrow (Fig. 5a). Owing to perspective distortion, this gradient changes with crab–burrow distance so that foraging crabs would need to use a few such cells, each tuned to a certain range of crab–burrow distances (Fig. 5b). We suggest that the crabs use the state of their path integrator² to select which of these neurons (or which combination) is most appropriate for the current crab–burrow distance.

For the crab's second task, namely to decide whether the dummy is approaching the burrow or not, there are two alternative solutions. The simplest solution would be to monitor the output of the distance neurons, because objects that approach the burrow would lead to an increase in their response. Alternatively, the directional selectivity could be achieved by appropriately aligned local motion detectors serving as input elements to the distance neurons, in a

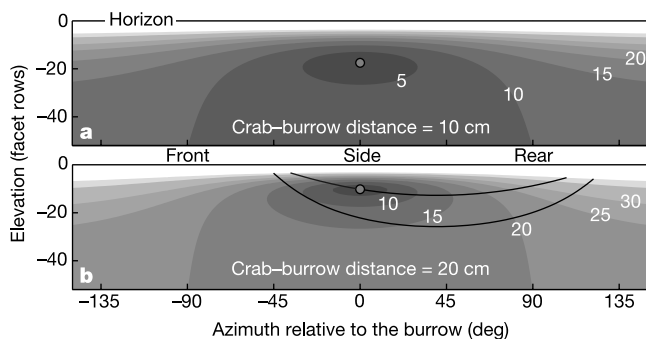


Figure 5 The effect of the crab–burrow distance on the mapping of concentric circles around the burrow onto the ommatidial array of a fiddler crab eye^{13,14}. The x axis shows azimuth in degrees, the y axis shows elevation in units of horizontal facet rows. The scaling is such that individual ommatidia take up equal space along both axes. Contours have been drawn for concentric circles with a radius of 5, 10, 15, 20, 25, 30, 40 and 50 cm. The distance map is shown for crab–burrow distances of 10 cm (a) and 20 cm (b). Two example dummy paths (unbroken lines), with a track angle of 50° and a track distance of 0 and 10 cm respectively, are also shown in b.

similar way to neurons involved in optic flow processing¹⁰. In the predictable visual environment of fiddler crabs, the difficult problem of measuring the distance between two distant objects, irrespective of the viewing angle, can thus be solved by a relatively simple matched neural filter¹¹. □

Methods

Apparatus

Crab dummies consisted of small black or white plastic cylinders with a width of 1.5 or 2.25 cm and a height of 0.8, 1.2, 1.6 or 2 cm. We carried out 484 of the total 633 experiments with a dummy size of 2.25 × 1.2 cm (width × height). The dummies were mounted on a thin, transparent perspex sled with the same width as the dummies, but twice the length to allow smooth motion on the ground. The dummies were moved along a straight line, the 'dummy track', by manually pulling on a monofilament line, which was fed around two tent pegs. The dummy movements could thus be controlled by an observer sitting about 5–6 m away. The dummy speed was roughly constant for a given experiment and ranged from 3 to 14 cm s⁻¹ between experiments (mean ± s.d. 7.8 ± 1.9 cm s⁻¹). We moved the dummy 10 cm past a focal crab's burrow but also monitored the reactions of neighbouring crabs by filming an area of about 1 m² around the focal crab's burrow from above. The crabs very quickly and fully habituate to the presence of both the camera and the observer.

Image analysis

On the basis of the x and y coordinates of the crabs, the dummy and the burrow, a response was considered to have started in a given frame if a crab moved at least 0.66 cm towards its burrow in the 240-ms time interval preceding this frame and at least 2 cm over a three-frame interval (720 ms) starting at the previous frame. We only analysed crab responses when the resident crab was at least 5 cm away from its burrow at the time of reaction. Our final analysis includes 633 dummy presentations from 25 animals. The crabs reacted in 493 of these experiments; however, responses were only counted if the crab reacted before the dummy had reached its closest point to the burrow for the first time (419 of the 493 responses or 85%). This was necessary because of the 74 late reactions, most of which (60) happened after the dummy turned around at the end of the track to move back to its starting position. The analysis in Fig. 4 is based on these late reactions.

Statistics

All of the statistical models used in this analysis allowed us to account for the repeated dummy presentations per crab (crab-to-crab variation). The significance of individual terms in all models was tested by calculating the Wald statistic associated with dropping the term from the model. To test for factors that influence the crabs' probability of response, we used the GLMM¹² in Genstat v4.2 (VSN International Ltd). No interactions reached significance and the final model had the following form ($n = 633$, $\text{Logit}(p) = \log(p/(1 - p))$): $\text{Logit}(p) \approx \beta_0 + \beta_1(\text{track distance}) + \beta_2(\text{track angle}) + \beta_3(\text{crab side}) + \beta_4(\text{presentation repeat}) + \text{error}$. The effect of track distance (d.f. = 1, Wald/d.f. = 15.64, $P < 0.001$) is fully discussed in the text. Decreasing track angles (see Fig. 3a) led to a decrease in the reaction probability from 70–80% for angles larger than 100° to about 40% for dummies that approach from beyond the burrow (d.f. = 8, Wald/d.f. = 4.89, $P = 0.001$). The response probability was about 10% higher for experiments in which crab side (see Fig. 3a) had a value of 1 (d.f. = 1, Wald/d.f. = 5.71, $P = 0.017$). Response probability decreased over 50 presentations from over 80% to about 40% (presentation repeat, d.f. = 5, Wald/d.f. = 5.47, $P < 0.001$).

To examine the response timing, we carried out a restricted maximum likelihood analysis (REML) using Genstat v4.2 that resulted in the following model ($n = 419$; Fig. 3): $\log(\text{dummy–burrow distance}) \approx \beta_0 + \beta_1(\text{track distance}) + \beta_2(\text{crab–burrow distance}) + \beta_3(\text{track distance} \times \text{crab–burrow distance}) + \beta_4(\text{presentation repeat}) + \beta_5(\text{track angle}) + \beta_6(\text{crab side}) + \text{error}$. The effects of track angle (d.f. = 8, Wald/d.f. = 2.15, $P = 0.028$) and the interaction between track distance and crab–burrow distance (d.f. = 1, Wald/d.f. = 12.67, $P < 0.001$) are discussed in the text. The effect of crab side (d.f. = 1, Wald/d.f. = 3.76, $P = 0.053$) was a small, 2.6-cm increase in the response distance (see Fig. 3b). Response distance decreased with presentation repeat from 31 cm to 21 cm over the course of 50 presentations (d.f. = 5, Wald/d.f. = 7.16, $P < 0.001$).

Neither the dummy brightness (black or white) nor the dummy speed had any influence on the response probability (GLMM: Wald/d.f. = 0.18, $P = 0.67$; Wald/d.f. = 2.75, $P = 0.10$) or on the response timing (REML: Wald/d.f. = 0.59, $P = 0.44$; Wald/d.f. = 0.31, $P = 0.58$).

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An active DNA transposon family in rice

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The publication of draft sequences for the two subspecies of *Oryza sativa* (rice), *japonica* (cv. Nipponbare) and *indica* (cv. 93-11)^{1,2}, provides a unique opportunity to study the dynamics of transposable elements in this important crop plant. Here we report the use of these sequences in a computational approach to identify the first active DNA transposons from rice and the first active miniature inverted-repeat transposable element (MITE) from any organism. A sequence classified as a *Tourist*-like MITE of 430 base pairs, called *miniature Ping* (*mPing*), was present in about 70 copies in Nipponbare and in about 14 copies in 93-11. These *mPing* elements, which are all nearly identical, transpose actively in an *indica* cell-culture line. Database searches identified a family of related transposase-encoding elements (called *Pong*), which also transpose actively in the same cells. Virtually all new insertions of *mPing* and *Pong* elements were into low-copy regions of the rice genome. Since the domestication of rice *mPing* MITEs have been amplified preferentially in cultivars adapted to environmental extremes—a situation that is reminiscent of the genomic shock theory for transposon activation³.

Rice is the most important crop for human nutrition in the world. At 430 megabase pairs (Mb), it also has the smallest genome among the agriculturally important cereals (including maize, sorghum, barley and wheat)⁴. For these reasons, rice is the focus of several genome-sequencing projects^{1,2,5}. Computer-assisted analyses of rice genomic sequence indicate that, despite its small size, over 40% is repetitive DNA and most of this is related to transposable elements^{1,2}. The class 1 long-terminal repeat (LTR) retro-

transposons comprise the largest component of transposable elements in the rice genome (14% of the genomic DNA) but, numerically, MITEs form the largest group with over 100,000 elements divided into hundreds of families comprising about 6% of the genome^{6,7}. MITEs are the predominant transposable element associated with the non-coding regions of the genes of flowering plants, especially grasses, and have been found in several animal genomes including *Caenorhabditis elegans*, mosquitoes, fish and human (reviewed in ref. 8).

Structurally, MITEs are reminiscent of non-autonomous DNA (class 2) elements with their small size (<600 base pairs) and short (10–30 bp) terminal inverted repeats (TIRs). But their high copy number (up to 10,000 copies per family) and target-site preference (for TA or TAA) distinguish them from most previously described non-autonomous DNA elements⁸. Non-autonomous elements, which make up a significant fraction of eukaryotic genomes, have been classified into families according to the transposase responsible for their mobility. But classifying MITEs in this way is problematic because no actively transposing MITE had been reported in any organism. Instead, the tens of thousands of plant MITEs have been classified into two superfamilies on the basis of the similarity of their TIRs and their target site duplication (TSD): *Tourist*-like MITEs and *Stowaway*-like MITEs^{7,9,10}. Much evidence links *Tourist* and *Stowaway* MITEs with two superfamilies of transposases, *PIF/Harbringer* and *Tc1/mariner*, respectively^{9–11}.

Because newly transposed elements should be identical, we considered that an active MITE family would be characterized by extremely low intrafamily sequence divergence. The availability of almost half of the Nipponbare genome (187 Mb by 24 December 2001) in public databases (<http://rgp.dna.affrc.go.jp>) provided the possibility of searching for repeat families with the structural features of MITEs and with very low intrafamily sequence divergence. We first identified 1,257 repeat families with RECON¹², a program for the *de novo* identification of repeat families. Manual inspection of these sequences subsequently indicated that a repeat of 430 bp named *mPing* was a candidate for an active MITE. The TSDs (the trinucleotide TAA or TTA) and TIRs of *mPing* indicated that it is a *Tourist*-like MITE (Fig. 1). Of the 36 independent copies mined from 270 Mb of Nipponbare sequence, 26 were identical. By contrast, only eight complete copies of *mPing* were found in the 361 Mb of contig sequence of the *indica* cultivar 93-11 (ref. 2). From the frequency of elements recovered per megabase, we estimated the whole genome of Nipponbare and 93-11 to contain 70 and 14 copies of *mPing*, respectively (Methods).

The only rice transposable elements shown previously to be active are three families of LTR retrotransposons (*Tos10*, *Tos17*, *Tos19*) that transpose in both *japonica* (Nipponbare) and *indica* (C5924) cell culture¹³. To assess whether *mPing* elements are activated in the same cell lines, we used a modification of the AFLP technique called transposon display^{14,15} to detect *mPing* insertions that might have occurred in culture. Because all of the *mPing* elements were virtually identical at their ends (Fig. 1 and Supplementary Information), we designed element-specific primers located in subterminal sequence (Methods) to amplify all family members and the flanking sequence.

The number of polymerase chain reaction (PCR) products (referred to as amplicons) amplified from DNAs isolated from Nipponbare (*japonica*) and C5924 (*indica*) plants before culture was consistent with the copy-number estimates for these cultivars (Fig. 2a); however, a differential response to cell culture was observed. Whereas the Nipponbare amplicon pattern remained the same, C5924 cells have undergone a marked increase in amplicons. Nonspecific genomic rearrangements during cell culture were ruled out as a cause of the pattern differences by repeating transposon display with primers derived from two other rice transposable elements (a *gypsy*-type LTR retrotransposon (SZ-2; N.J. and S.R.W., unpublished data) and a MITE (*ID-1*; ref. 7). In