Exploring with damaged antennae: do crayfish compensate for injuries?

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Summary

Appendages are important sources of sensory information for all animals that possess them but they are commonly damaged in nature. We describe how the tactile system of the crayfish *Cherax destructor* functioned when subjected to the kind of damage found in wild-caught or cultured animals. Touch information was methodically varied by the removal of antennae and chelae. The resulting behaviour was analysed in a T-maze. Crayfish with a single antenna ablated turned toward the intact appendage, however, those with only a partial ablation did not, suggesting that a tactile information threshold exists for normal behaviour. When exposed to the same environment after an antennal ablation but with no prior experience in that terrain, crayfish also turned toward the side of the intact antenna. By contrast, when animals with experience obtained in a previous trial with intact antennae were tested after ablation of one antenna, they did not turn into one arm of the maze more than the other. These two outcomes indicate that behaviour is affected by an interaction between the time at which an injury occurs and an animal's knowledge of the topography, and that an injury may affect learning. We also tested to see if other appendages could provide tactile information to compensate for antennal loss. Input from the chelae did not affect the turning behaviour of crayfish in the maze.

Key words: crustacea, haptic systems, learning, touch.

Introduction

Aquatic benthic environments are regions of transition between the solid and fluid worlds. Animals must adapt to the high turbulence, low light levels and minimal visibility that typify this region (Puckridge et al., 1998; Fine-Levy and Derby, 1999; Thoms and Sheldon, 2000; Grasso and Basil, 2002). The capacity to explore in the dynamic conditions of the zone may provide selective advantage for many organisms. Advantageous adaptations for such activity are likely to rely heavily on non-visual stimuli (Kaplan et al., 1993) because, in the absence of visual input, other modalities become more important. Sound, chemical and tactile (touch) cues can be used to collect information (Webster and Weissburg, 2001). Of these, touch information and chemosensory input are likely to play a major role in exploratory behaviour (Taylor, 1975; Tautz et al., 1981).

Many adult crustaceans are benthic. Much is known about how they interpret chemical cues in their environment (e.g. Hazlett, 1971; Reeder and Ache, 1980; Derby and Atema, 1982; Beglane et al., 1997; Derby and Steullet, 2001; Kraus-Epley and Moore, 2002; Cate and Derby, 2002a; Cate and Derby, 2002b). Less is understood about how they use tactile information. Research in this field has focused on how it is used for prey location. Zeil and colleagues (Zeil, 1985) discovered that both sighted and blind crayfish use their antennae to locate small stationary objects, such as mussel shells. Crayfish also orient themselves to swimming fish prey with their antennae (Breithaupt et al., 1995). Tactile cues are likely to be used for more behaviours than these, such as shelter search and territory exploration, but there is limited information on such exploratory activities [shelter (Alberstadt et al., 1995), exploration (Basil and Sandeman, 2000; Patullo and Macmillan, 2006)].

The second antennae provide much of the touch information available to decapod crustaceans (Tazaki, 1977; Vedel, 1985). In most crayfish, the antennae are flexible, tapered and almost as long as the animal's body (e.g. Sandeman, 1989). Each antenna consists of five short proximal segments (the base) supporting a long, multi-segmented flagellum (Tazaki and Ohnishi, 1974; Sandeman, 1985; Zeil et al., 1985). The antennae assess position, movement, direction and velocity of one segment relative to the next (Hartman and Austin, 1972; Sigvardt, 1977; Zeil et al., 1985; Sandeman and Varju, 1988).

Tactile information appears to be derived mainly from the active movement of sensory appendages. Walking crayfish wave their antennae back and forth through horizontal angles of 100° or more relative to the long axis of the body (Sandeman and Wilkens, 1983; Zeil et al., 1985; Breithaupt et al., 1995). This active movement resembles that of other tactile systems that require active touch or tactile scanning (Gibson, 1962; Zeil

et al., 1985). Tactile scanning requires mobility of the sense organ, and the capability to discern the position of the sense organ in relation to the body (Sandeman, 1985). A sense organ with these two properties allows an animal to estimate the angle of the sense organ relative to its body, and the distance between the body and objects in its path. This information can then be combined or compared (McMahon et al., 2005), and allows the animal to form an image of the three-dimensional layout of their environment (Zeil et al., 1985). This is particularly relevant when animals explore new terrain (Basil and Sandeman, 2000; Patullo and Macmillan, 2006).

Given that the antennae are important in forming an image of the environment and in other behaviours, it could be advantageous for them to remain functional for the entire life of the animal (Harrison et al., 2001). However, the proximity of antennae to danger (Bovbjerg, 1956), and their mobility, makes injury likely. Crayfish, and other crustaceans, have the capacity to regenerate antennae (Harrison et al., 2001), but it takes time for an injured appendage to become indistinguishable from the original, sometimes more than 6 months (Harrison et al., 2001; Hartman and Cooper, 1994). It is therefore likely that for periods in an animal's life its sensory and locomotory appendages are not intact.

Individuals with incomplete, or non-functional, sensory appendages may be disadvantaged. How crayfish accommodate such situations is not fully understood. There is some evidence that reduced tactile information changes their behaviour. Crayfish of the species *Cherax destructor* with one flagellum denervated favour searching toward the intact side (McMahon et al., 2005). When both flagella are severed at the base, the animals no longer walk close to surfaces that provide tactile information (Basil and Sandeman, 2000). These results support the hypothesis that the antennae are the primary tactile appendages used in exploration so that any damage to them could be disadvantageous.

Crayfish may be able to offset lost tactile input by compensating with information from other sources besides the antennae in the same way that other arthropods compensate for lost appendages until they have regrown (Blazis and Grasso, 2001). Derby and Steullet proposed that multiple sensors act to maintain the function of some sensory systems in the face of damage and compensate for non-functioning developmental sensor stages (Derby and Steullet, 2001). It is largely unknown whether compensatory mechanisms operate in crayfish tactile systems. Mechanoreceptive setae, which cover almost all body surfaces, including the chelae and the dactyls (Tazaki and Ohnishi, 1974; Tautz and Sandeman, 1980; Solon and Kass-Simon, 1981), may provide alternative sources of information. A familiar environment could also help. Crayfish are capable of learning local topography in a short period of time (Basil and Sandeman, 2000; Shuranova et al., 2005). Individuals that know an area may therefore be able to navigate through it successfully on subsequent visits with less than normal tactile information.

The goal of this study was to provide insight into how crayfish with injured antennae behave and whether or not they can compensate for the lost information. Appendages were ablated to simulate damage that occurs in the wild. Four objectives were addressed: (1) how the complete or partial loss of antennae affects exploratory behaviour; (2) whether search strategy changes during repeated exposure to the same environment after damage to the antennae; (3) whether prior experience in an environment can compensate for exploration with damaged antennae; and, (4) whether other appendages can provide tactile information to compensate when both antennae are damaged.

Materials and methods

Australian freshwater crayfish, *Cherax destructor* (Clark), 5–9 cm in length (rostrum to tailfan) were obtained from commercial suppliers. Individuals were housed in upright cylindrical enclosures (PVC tubes; 11 cm inside diameter, 12 cm high). Six holes (0.5 cm diameter) were drilled around the base, 1.5 cm from the bottom. This allowed water and chemical signals to flow between tubes, but isolated animals to prevent fighting and injury. Enclosures were placed in large fibreglass aquaria that allowed approximately 45 animals to be kept together. Crayfish were acclimatised to a 12 h:12 h reverse light:dark cycle for 5–8 days before experiments. Only experimentally naïve animals with all appendages intact were used.

Apparatus

Experiments were conducted in a tubular T-maze constructed from PVC pipe (10 cm diameter). This apparatus is briefly described here, and in more detail by McMahon et al. (McMahon et al., 2005). Two 55 cm long side arms were joined to a 120 cm long entrance arm with a T-joint, and capped (Fig. 1). A 3 cm wide cut-out was made in the top of the maze. Crayfish placed in the base of such a maze navigate their way to the top and turn into one of the arms (McMahon et al., 2005). Individuals could simultaneously touch both side walls of the maze with their antennae and walked up the centre.

A CCD camera (Jaycar) mounted 30 cm above the junction of the T-maze filmed trials. Camera footage was displayed on a monitor and recorded to tape by a video cassette recorder. Videotapes were viewed post trial on a 68 cm television to collect behavioural data and minimise any observer bias.

Procedure
Operations

Four experiments were conducted with combinations of operated and unoperated animals. Other research has taken a similar approach to investigate the control of decapod behaviour (e.g. Beglane et al., 1997; Basil and Sandeman, 2000; McMahon et al., 2005). Tactile information available to crayfish was systematically altered by the removal of antennal flagella and chelae. The ablations simulated damage that occurs in the wild, e.g. severing of an antenna by an opponent's chelae during a fight or autotimising a cheliped to escape. Crayfish
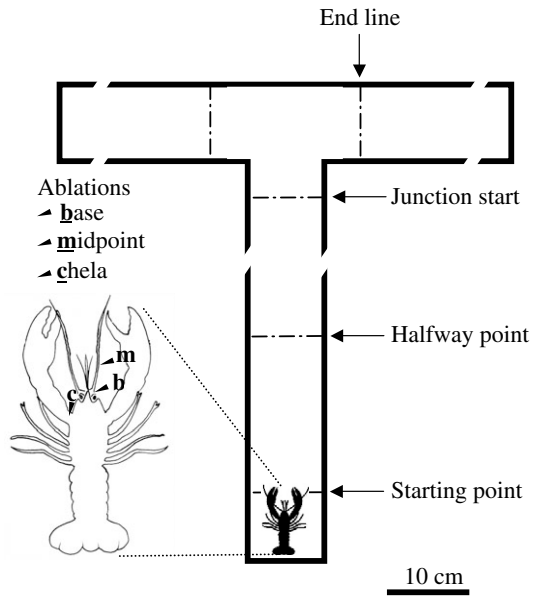
Fig. 1. Animals were placed at the base of the maze. A trial began when the crayfish crossed the starting point. Individuals moved up the maze, past the halfway point, to the junction start. Trials ended when the crayfish crossed the end line. Crayfish inset indicates ablation points with arrowheads.

were anaesthetised by immersion in crushed ice for 30 min prior to surgery. The location of the operation and the timing of the maze testing in relation to the surgery are outlined below and in Figs 1 and 2.

Animals were randomly assigned one of four ablation types.

(1) Antennal base. One flagellum was severed at the base between the first and tenth annuli. This removed the flagellum but left the basal proprioceptors intact. The animal received no mechanosensory input, but position information was still available from the basal segments. (2) Antennal midpoint. The ablation occurred between the 50th and 60th annuli distal to base. This standardised the amount of flagellum animals had, and thus reduced, in a controlled manner, the amount of tactile input the animal received. It resulted in an antenna that was shortened to approximately 25 mm in length (intact antennae are about 60 mm for these sized crayfish). (3) Chelae. Each chela was held immobile and a pair of fine scissors was used to cut into the animal's exoskeleton immediately distal to the autotomy plane, at the seam between the basis and the ischium (see Wood and Wood, 1932; Bliss, 1960; McVean, 1975). This caused the animal to autotomise its chela, and allowed the wound to seal and heal quickly and cleanly. (4) Sham. To control for any operational effects, groups of crayfish were treated identically to other operated animals but the appendages were not severed.

For experiments in which only one of a pair of appendages was ablated, individuals were randomly assigned to left or right side treatment. Crayfish were allowed 1 day to recover before a trial in the T-maze.
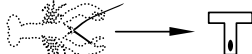
Trials in the maze

Trials commenced approximately 30 min after the onset of dark, and continued for 3–4 h. Crayfish are mainly nocturnal and there is evidence in some species that this is the most active period (Page and Larimer, 1972). Red light illuminated the experimental room (fluorescent tube with red filter, light levels
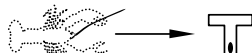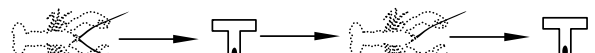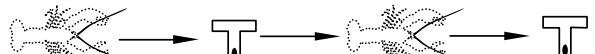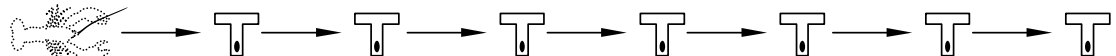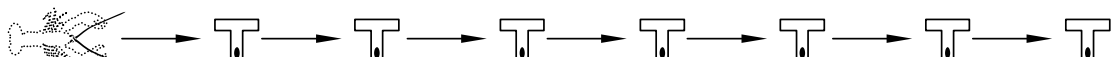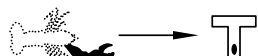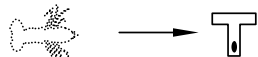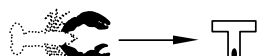

Fig. 2. Summary of the experiments. Crayfish are pictured with antenna and chela ablations with respect to the points when tests occurred in the maze. Legend bottom right indicates treatments.

of less than 1 lux at maze level). This allowed the experimenter to view animals and facilitated filming, but prevented animals receiving visual cues. Behavioural tests show that crayfish behaviour is unaffected by movement at such light levels (McMahon et al., 2005).

A crayfish was removed from its housing tube by net and placed in an empty plastic container ($20 \times 20 \times 10$ cm) for 6 min. It was then tipped into the base of the T-maze (starting point, see Fig. 1). Observations began when the rostrum of the crayfish crossed the starting point in a forward direction. Trials ended when the rostrum crossed the end line located 5 cm from the junction in one of the side arms (end line, see Fig. 1). Previous research showed that once a crayfish crossed this point it remained in that arm (McMahon et al., 2005). Animals were given 10 min to complete the task. Individuals that did not reach the end of the maze in that time were noted but excluded from analysis. Following each trial, the maze was cleaned twice with a high-pressure hose and refilled.

Experiments

Experiment 1

To examine how complete and partial loss of a flagellum affects behaviour, two ablation points were used: basal and midpoint. Forty five crayfish were in each of these treatment groups.

Experiment 2

To investigate whether recent experience in an environment before sensory loss allows an animal to compensate for subsequent loss of antennae, animals were run through the maze prior to the operation. Two groups of 40 crayfish were assigned to a treatment and control. The crayfish were run once in the T-maze 5 days prior to their operation or sham treatment. Operated animals had an antenna severed at the base and control crayfish remained intact.

Experiment 3

To determine whether repeated exposure to the same environment after ablation would allow animals to compensate for lost antennal information, two groups of 45 crayfish were run in the maze seven times. 'Basal' animals had one flagellum severed at the base and control animals remained intact. Animals were run through the T-maze after the recovery period and then again 5, 10, 15, 20, 25 and 30 days post operation.

Experiment 4

To test whether information from other appendages is used by crayfish to compensate for reduced antennal input, chelipeds were ablated at the same time as both antenna were ablated. The chelae were selected because they have tactile receptors and are positioned on either side of the body so they may provide directional information in the maze. Three experimental groups of 45 animals were used: no chelae, one chela, control. The control group was handled to simulate the ablation of two chelae, whereas the one-chela group had one

chela severed, and the no-chelae treatment group had both chelae ablated.

Data analysis

In all experiments, the number of animals that turned in different directions (left or right arm) was compared. For operated animals, the direction turned was referenced to the ablated flagellum to give a score of either toward or away from the intact side. These binomial data were analysed using Yates corrected χ^2 tests, as there were only two possible outcomes (Sokal and Rohlf, 1995). Previous experiments with large populations of intact animals show that crayfish display unbiased turn behaviour in this maze (McMahon et al., 2005). Values were therefore compared to an expected outcome of an equal number of turns into the two arms. Groups of control animals were run throughout the experiments to confirm this and ensure that some seasonal or sample bias was not present. A Wilcoxon sign rank test was performed on the repeated experience data to see if the ablated animals turned consistently in the same manner as the shams (Sokal and Rohlf, 1995). Time (s) spent travelling to, and in, the junction were compared between treatments in each experiment with ANOVA or two sample t-tests. Data were compiled using Microsoft Excel 2000 and analysed in Minitab v13.20 or Systat v11. P-values of less than 0.05 were considered significant.

Results

Intact animals

Intact crayfish displayed a common behaviour pattern. Individuals spread their antennae to touch the side walls prior to walking. They then travelled up the entrance arm with the antennae contacting the wall. When they reached the maze junction, they scanned briefly in both directions with their antennae before turning into one side arm. Animals waved their antennae in front of them while they walked, sensing the area immediately ahead of them. Intact animals displayed no difference in the number of turns in the two directions when presented with a T-maze in which they had no experience. Of 80 crayfish tested during the experiments, 41 turned left, while 39 turned right ($\chi^2=0.013$, $P=0.909$). These results verify that intact crayfish use a random search strategy in this maze environment (McMahon et al., 2005) and confirm the control status of this cohort of animals.

Partial or total antennal ablation

Animals with one base-ablated antenna held the intact antenna ahead of them, the base of the severed antenna also appeared to be held ahead. Crayfish with one antenna ablated at the base displayed a significant bias in the direction turned at the junction. Thirty-four crayfish turned toward their intact antenna and 10 away ($\chi^2=12.023$, $P<0.001$). Individuals with one antenna ablated at the midpoint displayed no bias in their turns. Fifteen animals turned away from their intact side, whereas 27 turned toward that side ($\chi^2=2.881$, $P=0.089$).

One traverse of the maze prior to antennal ablation

Prior to the operation, both groups of animals displayed no turn bias. Seventeen turned left and 21 turned right (χ^2=0.237, P=0.626) in one group, and 16 turned into the left arm and 19 turned right in the other treatment (χ^2=0.114, P=0.736).

The performance of these animals was the same when placed in the maze a second time, after the operation or sham. Of the animals with one ablated antenna, 22 turned toward their intact side and 13 turned away from that side (χ^2=1.829, P=0.176). Fourteen control animals turned left, 17 turned right (χ^2=0.129, P=0.720).

Repeated traverses in the maze after antennal ablation

Animals with one ablated antenna were more likely to turn towards the side of their intact antenna over the 30 days of observation (Wilcoxon rank: Z=–2.197, P=0.028; Fig. 3A).

Ablating other appendages

Crayfish with both antennae ablated, as well as selectively ablated chelae, turned into both maze arms. Of the control animals with both chelae intact, 23 animals turned left and 14 turned right (χ^2=1.730, P=0.188). In animals with one chela ablated, 23 turned away from their intact chela, 11 turned toward it (χ^2=3.559, P=0.059). Of the animals with both chelae ablated, 20 turned left and 18 turned right (χ^2=0.026, P=0.872).

Temporal aspects of exploration

The control cohort of animals walked to the junction in 21.0±29.9 s (mean ± s.d.) and were in the junction for 7.8±4.4 s before crossing a decision line. The travel time of crayfish in the four experiments was not influenced by the injuries (P>0.05; Figs 3B, 4). In the repeated traverse experiment (no. 3), the time in which crayfish walked to the start of the junction was different across the 30-day testing period but this was for both treatments (P=0.049; Fig. 3B).
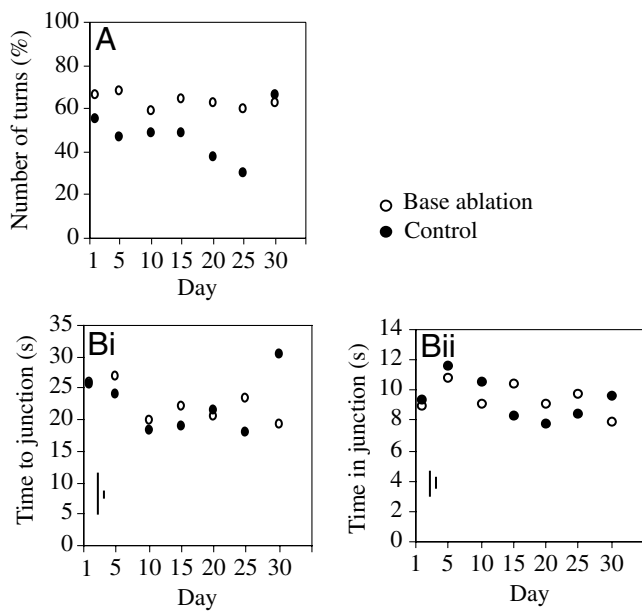
Fig. 3. Repeated traverses in the maze summary (experiment 3). (A) The number of turns toward the side of the intact antenna of crayfish with one flagellum ablated, and the left side (randomly selected) of the controls, across the 30-day experimental period. Ablated animals were different to the control (Wilcoxon: Z=–2.197, P=0.028) and the number of turns was generally greater in the ablated animals than those in the control. (B) Time in the maze for crayfish with intact (control) or a base ablated antenna. (Bi) Mean time to walk to the start of the junction varied across the 30-day period (P=0.049) with trials from day 10 onwards generally faster than those in the first two tests. There was no difference in time variation between the treatments (P=0.069, interaction term F=0.00, P=0.986). (Bii) Time to move through the junction was not different between the treatments (2 factor ANOVA all terms P>0.05). Error inset lower left (range of 1 s.e.m.).

Fig. 4. Summary of movement times (mean + 1 s.d.) of crayfish to and through the junction of the maze, (A) after antennae midpoint or base ablation (experiment 1); (B) before and after ablation of one antenna (experiment 2); (C) after chelae ablation (experiment 4). No differences were detected between the treatments in the three experiments (time to junction Exp. 1: $T_{(24)}$=0.94, P=0.349; Exp. 2: P>0.05 for all ANOVA terms; Exp. 4: $F_{(2,101)}$=1.27, P=0.286; time in junction Exp. 1: $T_{(24)}$=1.08, P=0.284; Exp. 2: P>0.05 for all ANOVA terms; Exp. 4: $F_{(2,101)}$=0.67, P=0.515).

Discussion

How would reduced antennal tactile input affect behaviour in the wild?

The total removal of one antenna had a pronounced effect on arm choice by naïve animals exploring the maze. When an antenna was ablated, *C. destructor* favoured the side of the intact flagellum. This suggests that complete loss of an antenna in the wild habitat, through fighting or otherwise, may reduce the effectiveness of exploratory behaviour in unfamiliar environments. It is consistent with the results of a study showing that crayfish with one antennal nerve severed, but the flagellum otherwise undamaged, favour the intact side (McMahon et al., 2005).

When part of one antenna was removed, *C. destructor* did not display a turn bias toward the intact side. This suggests that a reduced level of information is sufficient for normal exploratory behaviour. In these trials, the percentage of crayfish that turned toward the intact side was similar to that observed in the base ablated animals. This suggests there may be a threshold of tactile information required for normal exploratory behaviour and that our partial ablation placed the animals close to that point.

There is some evidence that varying the sensory input also influences temporal aspects of crayfish exploration. Walking speed in a maze is increased by the selective removal of antennal input (McMahon et al., 2005). On the other hand, there is also evidence that the selective removal of chemical input from antennules results in slower locomotion (Kraus-Epley and Moore, 2002). The results of this study fall somewhere between these two outcomes. Walking speed was the same for all treatment groups within each experiment. It may be that the large variation in walking speed of the animals in this study prevented the detection of differences.

Does experience compensate for lost antennae?

Antennal damage affected behavioural outputs of *C. destructor* but prior knowledge also affected the outcome. If the antennal ablation occurred prior to exploring the area, the animal's search strategy was affected, whereas if the crayfish had previously explored the environment with intact appendages, subsequent injury did not affect turn behaviour. This agrees with studies that indicate sensory input available at the time new environments are encountered influences behaviour (Basil and Sandeman, 2000; Patullo and Macmillan, 2006). This would therefore also affect learning processes. *C. destructor* and other species of crayfish can learn the topography of an environment (Basil and Sandeman, 2000; Shuranova et al., 2005). This is also inferred from our results where crayfish generally walked faster to the junction after the first two trials (experiment 3; Fig. 3). In the maze environment, however, learning does not appear to affect turning behaviour of intact individuals (McMahon et al., 2005). Injured crayfish with repeated exposure to the same environment in our experiments turned in a biased manner. Together, these results suggest that some learning

does occur in this situation and that this was affected by antennal injuries.

In a wild environment, narrow and open spaces exist depending on how debris and substrate are positioned. When crayfish with ablated antennae walk around a larger, more open arena than the maze in this study, they do not dishabituate to the environment as they do when the antennae are intact (Basil and Sandeman, 2000). This indicates that learning is inhibited in wider spaces. We observed a behavioural change in animals placed in the narrow maze with no prior experience. This suggests that crayfish may process tactile information from open and confined areas in a similar manner. We could therefore predict the same result as in our narrow maze in a familiar open arena. That is, animals that previously explored in an open environment without injury, would not change behaviour in a subsequent trial with a restrained or injured antenna.

Can other appendages and receptors be used to compensate for lost antennal information?

The chelae manipulations did not result in biased turning behaviour. If these appendages functioned as tactile receptors to replace lost antennal information, one would have predicted a change in turn behaviour when one cheliped was ablated. It is known that tactile receptor setae are located on the chelae (Tazaki and Ohnishi, 1974; Solon and Kass-Simon, 1981), so it is interesting that the bilateral ablations produced no result. This may have occurred because the chelae are closer to the carapace than the antennae so they have a smaller range to detect objects and would probably do so after the antennae in most instances. Therefore, even if they use a bilateral comparison method similar to that thought to be used by the antennae and antennules (McMahon et al., 2005), they would provide a less valuable system for assessing directional tactile cues. Although we concentrated our focus on a compensatory function, this suggests that the tactile systems of chelae operate in a different manner, or perhaps for different purposes, from the antennal tactile system. Behaviours such as the defence response (Glantz, 1974; Kelly and Chapple, 1990), which also involve the chelae, might be more strongly affected than exploration if chelae were injured.

There are some other observations of chelae use during exploration. When the antennae are immobilised, the dactyls touch walls, particularly when crayfish arrive at the corners of a large arena and the animals do not walk near the walls (Basil and Sandeman, 2000). Together with our results, this suggests that the chelae are not used to direct movement when the antennae otherwise would. In a larger, more open arena than our maze, slower velocities have also been recorded for *C. destructor* when the antennae are restrained (Basil and Sandeman, 2000). Although we did not measure velocity per se, it seems that we did not make that observation here because travel times to, and through, the junction were similar to the control cohort. Injured *C. destructor* may therefore be able to learn terrain, or use other tactile input (i.e. from the legs) to

contribute to path integration in narrow spaces in lieu of antennal tactile information.

Compensation for injury is possible in some arthropod species. For example, if the crab *Calinectes sapidus* loses only one cheliped, and the spider *Pardose milvina* loses one or two legs, measured behaviours do not differ from those of intact individuals (Brautigam and Persons, 2003; Smith and Hines, 1991). Individuals do, however, become significantly disadvantaged if further limb loss occurs. In some instances it has been highlighted that compensation can occur but this is insufficient to overcome the injury (Brock and Smith, 1998). Our study indicates that the tactile system of *C. destructor* can overcome minor injuries, such as partial antenna loss, but major damage, such as complete antenna loss, modifies behaviour.

Implications for tactile systems

Tactile systems used by arthropods to explore terrain vary in sophistication. Examples from several taxa describe several functions including following walls and surfaces as well as distinguishing between different textures [e.g. ants (Dussutour et al., 2005), cockroaches (Camhi and Johnson, 1999), crayfish (Patullo and Macmillan, 2006)]. Touch is probably important in other behaviours that require the body to be orientated in a particular way. One example is when aquatic decapods navigate or search in odour plumes. The process is largely governed by chemical cues (e.g. Reeder and Ache, 1980; Weissburg and Zimmerfaust, 1994; Kozlowski et al., 2003) but studies also suggest that a number of sensory inputs, such as vibration, could provide additional information (Weissburg and Zimmerfaust, 1994; Finelli et al., 1999; Horner et al., 2004). Decapods can navigate by magnetic fields [*Panulirus argus* (Lohmann et al., 1995)], orientate toward swimming and stationary prey items [*C. destructor* (Zeil et al., 1985), *P. clarkii* (Breithaupt et al., 1995)] and rear into defence postures [*Cambarus bartonii* (Kelly and Chapple, 1990)]. These are other possible behavioural situations that could combine tactile information with other cues.

Some issues about crayfish tactile exploration remain unclear. For example, whether the effects of antennal removal persist until moult, and therefore regeneration, is unknown. An experiment in which treatments consist of ablations at a set period before trial, with no animals trialled twice, may be appropriate to remove inherent experience effects. Behavioural outcomes are likely to be affected by the modalities in play, but how information from supplementary sources is integrated with tactile information is not fully resolved. For example, the way vision affects tactile exploration, and understanding how different modalities work together is important for understanding haptic systems of crustaceans and other taxa.

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