Going Underground:
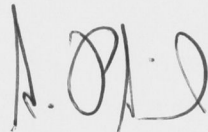# Predator Avoidance in *Uca vomeris*

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Acknowledgements

I would like to especially thank my supervisors at the Research School of Biological Sciences, Jan Hemmi and Jochen Zeil, for their support. I could not have finished this thesis without their strong and continued support. In many discussions they provided me with suggestions, helped develop ideas and provided encouragement during all of the project. Finally, I am grateful that they bore reading and correcting many of my preliminary thesis drafts.

Abstract

The predator avoidance behaviour of the fiddler crab *Uca vomeris* is organised in multiple response stages, which typically occur in sequence: freeze, home run, burrow surveillance, burrow entry, burrow time and resurfacing surveillance. Subsequent stages of this behaviour are likely to depend on information gathered during earlier parts of the response. This interdependency between consecutive stages makes analysis non-trivial because history effects have to be taken into account.

In this project, the crabs' responses to a simulated predator (called a bird dummy) recorded in field experiments by Jan Hemmi were analysed using two approaches, a non-linear time series analysis and a regression analysis using linear mixed-effects models.

The motivation to apply non-linear time series analysis to these data came from the consideration that history effects can be naturally integrated into this analysis and that the analysis does not require specific hypotheses. The analysis focused on the visual cues that lead to the decision to enter the burrow. I evaluated an unsupervised clustering method based on Real-Time Dynamical Systems Modelling [Webers and Zimmer 2005]. However, the performance of this method was unsatisfactory, as it was extremely sensitive to noise and variability in the data and because the dataset is comparatively small. Even though the proposed algorithm converged quickly, artifacts due to the end points of the time series made it difficult to draw firm conclusions.

The clustering algorithm was found to be unsuitable for this particular problem for three reasons. Firstly, the noise, inaccuracy and variability contained in biological data requires an analysis the outcome of which is not as sensitive to small changes in data and parameters. Secondly, the crab behaviour shows a number of discrete state changes where most of the interest lies in describing those changes and not in modelling the dynamics in between. Finally, the time series recorded for each response are too short and do not provide the quasi-periodic orbit-like series needed for steady-state analysis techniques.

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This approach was therefore supplemented with a statistical analysis using Linear Mixed-Effects Models. The history problem was resolved by reducing the analysis to cases where the previous history was similar. In the second part, I considered cues affecting home-run, burrow entry and burrow time.

The statistical analysis shows that

1. the crabs use different decision criteria and visual cues for different response stages. Home-run responses are triggered by a speed-sensitive cue, while burrow entry responses are triggered by a distance-specific cue. Burrow waiting time is depending on angular speed at the time of burrow entry.

2. the crabs distinguish approaching and departing predators. While crabs enter their burrow most frequently as the dummy approaches, they rarely do so when the dummy is moving away.

The results are discussed both with regard to the merits of the two approaches I used to analyse the data and with regard to the decision-making process underlying predator avoidance in fiddler crabs.

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Introduction

1.1 Crab Predator Avoidance Behaviour

Making good decisions about when to escape from a predator is essential for many animals. Flight behaviour is often costly but not fleeing imposes very high risks. In addition, gathering precise information about the predation situation is costly in terms of time and energy. Hence available information is often unreliable and imprecise [Fernandez-Juricic et al. 2004; Welton et al. 2003; Koops 2004]. I am interested in the way animals use visual cues to decide when and how to flee from a predator. A better understanding of this decision problem is likely to show how visual perception is adapted to a specific environment and has the potential to teach us how to tackle information gathering in similar environments.

Uca vomeris is a fiddler crab species that is found on the topical inter-tidal mud-flats of Queensland, Australia. The crabs live in individual burrows in mixed gender colonies. These burrows are the centre of a crab's territory and are defended against conspecifics. The crabs spend most of their life grazing in close vicinity to their burrows [Zeil and Hemmi 2006], which provides access to water, shelter from the tide and refuge from predators.

At this study site, the crabs' main predator is the gull-billed tern (*Gelochelidon nilotica*), a bird which travels at a height of about 2-3m across the mud-flat and dives down to pick up crabs [Land 1999]. Even though predators vary across fiddler crab species, in open mud-flats virtually all predators are either airborne or larger than the crabs. This allows crabs to identify predators by the fact that they will always appear above the visual horizon [Layne 1998]. Because the crabs carry their eyer on long stalks, the bodies of other crabs are in most cases below the visual horizon. The line of horizon thus provides crabs with a simple way of distinguishing predators and conspecifics, as it requires no information about the shape, size or actual position of an object.

In response to these birds and other approaching predators, the crabs seek refuge in their burrow. The crab's avoidance response can be subdivided into several distinct stages, whereas each stage is associated with different immediate costs, safety benefits and risks [Hemmi and Zeil 2005]. Firstly, a crab detecting a predation risk stops feeding and freezes on the spot (Freeze). This reduces conspicuousness and could potentially increase the crab's perception abilities by reducing self-induced image motion and blur.

In the next stage the crab runs part or all of the way home (Home-run). Running home makes the crab conspicuous, but being close to the burrow increases safety as the crabs can enter the burrow within a few hundred milliseconds if necessary. The home-run is likely to be energetically costly, being in motion will make it difficult to keep track of the predator's movement and position and the crab looses feeding time and social opportunities.

Having reached the burrow, the crab remains at the entrance (Burrow Vigilance). This time can be used to gather more accurate and detailed information about the predator,

such as distance and approach direction, while being in a position of safety. The costs associated with this stage are lost opportunity costs.

If the predation risk increases further, the crab enters the burrow (Burrow Entry). While in the burrow, the crab is safe. Nevertheless, this reaction is very costly. After entering the burrow, the crab looses information about the predator and may be attacked when resurfacing.

In the next stage, the crab spends time underground (Burrow Time) and needs to decide when to resurface. During this time, the crab cannot feed and interact with other crabs. It has to choose the time spent underground long enough to escape from predators that use a sit-and-wait strategy [Hugie 2003; Hugie 2004; Jennions et al. 2003].

After resurfacing the crab waits for a while at the burrow entrance before re-engaging in foraging activity (Re-surfacing Vigilance). This allows to reassess the current predation situation and the state of the environment.

It has been hypothesised that different stages in the crab's response are triggered by different visual cues [Hemmi and Zeil 2005]. Depending on the level of perceived threat [Jennions et al. 2003], social context [Reaney and Backwell 2007] and previous experience [Walker 1972; Hemmi and Zeil 2005], crabs do not necessarily display the entire response sequence. Therefore crabs have to decide which stage of the response to enter into and how to time the transitions between stages. Naturally this is based on the current assessment of the predation situation by the crab. Crabs perceive the predator using their eyes only, and therefore the risk imposed by the predator is determined by what crabs see.

So far, the visual cues that trigger the crab's home-run responses have been identified as being based on the angular speed of the predator in the crab visual field [Hemmi 2005a; Hemmi 2005b]. Cues eliciting the later stages of the crab response remain to be investigated. Understanding the decision criteria crabs use in their response allows us to find out about how the particular properties of their habitat shaped the crabs' vision system and their behaviour.

Related Work

2.1 Fiddler Crab Predator Avoidance

Fiddler crab escape behaviour has been an object of study for a long time. Visual cues have been studied as well as the influence of non-predation related factors on this behaviour.

A fixed increase in angular size has been stipulated as trigger for the home-run and underground reaction by [Nalbach 1990] in two crab species living in mangroves and mud-flats. His results were supported by electro-physiological recordings identifying cells that are sensitive to an increase in angular size of objects but not to expanding spiral patterns. A recent study [Oliva et al. 2007] showed that looming can elicit a home-run response in *Chasmagnatus granulatus* and identified a group of neurons through electro-physiology of which the firing rate is closely correlated with looming and the home-run speed. This is in contrast to [Hemmi 2005b], who showed that crabs respond to retinal speed as a cue for their home-run. The discrepancy can be explained by two different mechanisms determining the home-run response, an angular speed-based cue for stimuli with small angular size and a looming cue or a cue based on

increase of size for stimuli with large angular size, as the three experiments worked with dummies of very different sizes.

The flight of neighbouring crabs has been studied as a cue of triggering predator avoidance behaviour. [Russo et al. 1998] studied the reaction of *Dotilla fenestrata*, when wandering over the substrate in dense droves. He observed flight reactions by crabs which only saw an escape reaction of neighbours within a drove, but not his stimulus. Similarly, [Wong et al. 2005] showed that the fiddler crab *Uca pugilator* runs home, when a close neighbour is reacting to a stimulus only visible to the neighbour. However, burrow entry responses introduced by reactions of neighbours occurred only seldomly. *Uca pugilator* lives in burrows, therefore the home-run reactions could also be induced by the neighbour approaching the crab's burrow (as studied in [Hemmi and Zeil 2003a]) rather than as a predator avoidance reaction.

The decision process and evolutionary development leading to a waiting time strategy has been studied in [Hugie 2003]. This paper models predator-prey interaction as a game theoretic model and derives evolutionarily stable strategies, i.e. probability distributions from which predators and prey pick their waiting time during an encounter. These strategies have characteristics which are stable over a large parameter range. Therefore the author was able to verify his game-theoretic model in a later study investigating interactions between *Uca princeps* and the black-bellied plover *Pluvialis squatarola* in [Hugie 2004]. The study showed that crab and bird waiting times followed the distributions predicted from the game theoretic model during naturally occurring interactions.

Predator avoidance behaviour is influenced by habituation. While crabs are very

sensitive to new objects in their environment, they quickly habituate to repetitive stimuli elicited by the same object [Walker 1972; Hemmi and Zeil 2003a].

Time spent underground can be shown to be influenced by the predation situation. In experiments with simulated predators eliciting a burrow entry response in *Uca lactea perplexa*, [Jennions et al. 2003] observed longer waiting times for simulated predators close to the crabs in contrast to crabs far away. Flight responses for distance comparisons were caused by a person standing up and sitting down quickly close (0.5m) and far away (2.5m) from the crabs. The authors were not able to show a significant influence of direction of approach on re-emergence time, but their result suggests that crabs approached directly stay in their burrow for longer.

Also, mating behaviour has been shown to compete with predator avoidance, suggesting that predator avoidance takes into account costs incurred by lost opportunities. Studying the refuge use of *Uca mjoebergi* in response to a predator, males reduce time spent in the burrow in the presence of a receptive female [Reaney 2007]. Food levels did not have a direct influence on re-emergence times. Even though Reaney found re-emergence times to be shorter when food levels were naturally high during the semi-lunar tidal cycle, providing food additions while food levels were naturally low had no influence on re-emergence time.

Finally, refuge provision and risk-taking behaviour as a means of sexual preference and discrimination has been studied for crabs as well. Risk-Taking behaviour is linked with aggression and mating success in *Uca mjoebergi* [Reaney and Backwell 2007]. The construction of signposts, males of some species engage in, has been shown to be related to predator avoidance. Courting female *Uca terpsichores* were attracted to male

burrows and engage in mating behaviour, because the structures built by males serve as indication of a refuge from a predator [Christy and Backwell 2006] and [Kim et al. 2007].

Of course, avian predators are not the only predators preying on fiddler crabs (e.g. [Christy et al. 1998; Russo et al. 1998]), however I restrict my study to avoidance behaviour of *Uca vomeris* from avian predators as would be encountered in an open mud-flat.

Observations

3.1 Experimental Setup

Because of their close-set eyes and low resolution the crabs' stereo depth perception is limited to a few centimetres. Fiddler crabs respond to predatory birds when the birds are so far away (more than 5m) that the crabs do not have direct distance information. Also, the low resolution prohibits accurate shape recognition for distant objects. It is therefore possible to trigger the crabs' avoidance responses using small Styrofoam balls as dummies, which can be moved across the mud-flat much closer to the ground than a real predator would move. Size and speed of the dummy have to be compensated for to allow it to move at a similar range of speeds to a predatory bird [Hemmi 2005a].

Experiments with such dummy birds have been performed by Jan Hemmi in a fiddler crab colony close to Townsville between October 1st, 2005 and October 6th, 2005 with the aim of expanding earlier work, which was designed to unravel the sensory cues triggering the home-run response only. Crabs were recorded on video by three downward-looking cameras placed at approximately 1.6m above ground, each

Observations
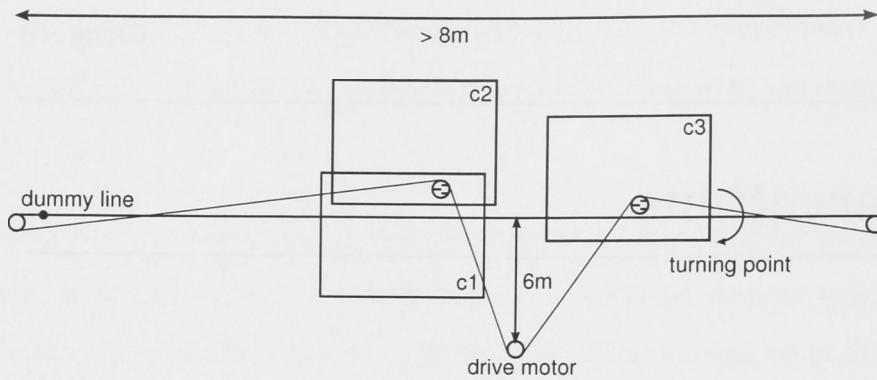
Figure 3.1: Setup of Experiment. The three rectangles shown represent camera views. The dummy line is strung between two poles and then wound over a motor and two wheels. Observing wheel rotation allows the dummy motion to be reconstructed even when the dummy is not visible in the camera. The figure is not to scale.

camera observing a patch of mud-flat of size 0.8m by 1.4m. Within the recording area of each camera, between 3 and 10 inhabited burrows could be seen.

The dummy was attached to a fishing line strung between two poles in the ground. It was moved at a height of 20cm above ground in a straight line over or close to the observed patch. Driven by an electrical motor, its speed was more or less constant.

A schematic drawing of the experimental setup is shown as a 2D projection in Figure 3.1. The three patches observed by the three different cameras are labelled c1 to c3. Not only does this setup allow to observe more crabs than with just one camera, but it allows to monitor responses of crabs that are not directly approached by the dummy using the one camera off to the side of the line (c2). The field of view of c1 and c2 overlap so both cameras record the movement of one monitoring wheel to track the movement of the dummy. However, no burrows are located in the areas that overlap. See also figure 3.2 which shows a reconstruction of an experiment performed on 5.10.2005.
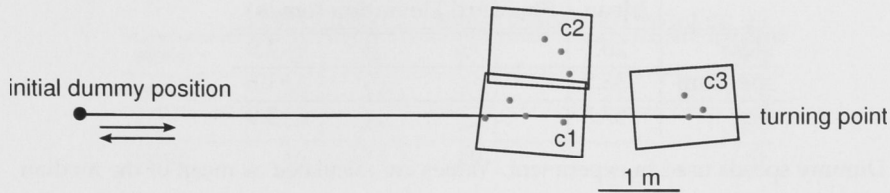
Figure 3.2: Reconstructed camera field of view (black rectangles), dummy line and burrow positions (gray dots) of one experiment. All positions are to scale, the burrow and dummy size are increased so they are actually visible.

3.2 Data Extraction

Crab, burrow and dummy position were digitised from the video material using a custom-made analysis program written by Jan Hemmi. The sequence was sampled at a rate of 5 frames per second (corresponding to a 200ms inter-frame interval). Where the dummy is not visible, its position is inferred from the rotation of a wheel attached to the fishing line.

In addition to crab position, transitions between behavioural categories were labelled. The following categories were used:

Re-surfacing The crab appears inside its burrow, i.e. the first frame in which any part of the crab is visible is recorded.

Burrow departure The crab breaks tactile contact with its burrow. After coming to the surface, crabs remain close to their burrows for a while, often touching it with one of their walking legs. If this breaking of contact is visible on video it is recorded, otherwise the frame in which the crab has moved more than 1.5 times its body length away from the burrow centre is considered the time of burrow departure.

	Mean	Standard Deviation (cm/s)
slow	20.1	4.9
medium	36.2	1.6
fast	67.8	3.9

Table 3.1: Dummy speeds used in experiment. Values are calculated as mean of the median speed of each run.

Burrow contact For complete home-runs, the frame is recorded in which the crab first makes contact with its burrow. This is defined as the frame in which any part of the crab's body gets closer to the burrow centre than $1.5 \cdot (crabsize + burrowradius)$

Burrow entry The frame of burrow entry is recorded. At this point in time one can be sure that the crab does no longer see anything about the world on the surface.

3.3   Procedure

Initially, the dummy was placed outside the field of view of all cameras at a distance of 4-6m from the setup. It was then moved forward, approaching the camera setup, passing all cameras. It reached an endpoint slightly beyond the field of view of the last camera. After resting at the endpoint for a short moment, the dummy was moved back to its initial position. Consecutive runs were performed when most of the crabs which had reacted to a previous presentation had resumed feeding (see Figure 3.3).

As these experiments were field experiments, escape responses were also caused by natural predators and other events. When a real bird passed close to the recording area and caused escape reactions, the experiment was interrupted until most of the crabs who had responded resumed feeding.

	Min	Max	Mean	Standard Deviation (s)
slow	67	100	85	8.4
medium	28	52	45	5.4
fast	19	28	24	2.6
gaps	35	171	80	31

Table 3.2: Length of dummy movements and gap between runs (all values in seconds).

Knowing the crab and dummy positions, the visual cues available to the crabs can be reconstructed. The retinal position and angular size of the dummy as seen by each crab can be calculated. In addition, considering the dummy velocity vector, angular speeds (in horizontal and vertical directions) can be calculated for each point in time.

Three different dummy speeds were used. Speeds are shown in table 3.1. Minimum, maximum and average lengths of runs using the three different dummy speeds as well as average time between runs are shown in table 3.2. In each experimental situation, crabs were subjected to 9 runs, where each dummy speed was used once in a 3 run interval block. The order of speeds within such a block was randomised. If during the recording of a sequence an error occurred, another block of runs was performed (12 runs instead of 9). The erroneous runs were discarded for analysis but still digitised to be able to keep track of the number of dummy presentations each crab had experienced.

The dataset analysed consisted of recordings from 5 different camera setups done on three days at different locations. Each setup provided three camera sequences, where each sequence showed between 3 and 10 crabs. Data from 66 crabs were recorded, which yielded 540 crab observations, where crabs were on the surface during some part of the run (302 of these were considered for the analysis in which they were away from their burrow at the beginning of a run). However, not all of these runs are

Response Stage	Observations	% responded
visible during run	540	
away from burrow	302	
home-run	262	87 %
burrow contact	193	64 %
burrow entry	188	62 %
burrow entry before dummy was past	129	43 %

Table 3.3: Number of observations recorded in the experiment. The third column shows the fraction of crabs that responded with respect to the number of crabs that were initially away from the burrow.

considered valid for later tests. The number of reactions observed is shown in table 3.3.

3.4   Classification of Reaction

The different behavioural stages described in Chapter 1 can be distinguished in the data set using a fixed set of rules. This is necessary to automatically and objectively classify a crab response.

Crabs are not always in a state where they could exhibit a certain reaction. For instance, if the crab is still at the burrow entrance, it cannot run home. Therefore runs which do not allow for a certain reaction were excluded from the analysis. This is the case for all crabs that at the beginning of the run were in contact with their burrow.

- The **freeze** stage of the crab response cannot be observed in the video recordings at all and is therefore not analysed.

- **Home runs** are considered a valid response if the following criteria are fulfilled:

  – A crab is moving for at least 3 frames (0.6s) towards its burrow

- A crab runs home for a distance of at least 20mm

- In each of the frames in which the crab moves, it moves faster than the minimal average speed, i.e. in each of the 3 frames it moves at least by $\frac{20}{3} = 6.67$ mm

A crab's home-run response is considered to have started in the frame before the first movement.

- Crabs are considered to have **entered the burrow**, if they are no longer visible inside the burrow. As they need some time to enter the burrow after deciding to disappear, their reaction is considered to have started 2 frames (i.e. 400ms) before they become invisible. Only runs were considered that showed a home-run before the burrow entry.

- **Re-Surfacing** is considered to have happened when the crab is visible in the burrow again. Crabs consistently need 2-3 frames until they have exited the burrow, but it is not clear at what point they can see the surrounding again from inside their burrow. This measure is therefore conservative. All recordings that were considered for the burrow entry response also were considered for re-emergence.

At the end of extraction the data schematically look like the traces shown in Figure 3.3. Initially, the crab is outside its burrow. When the dummy starts moving, it approaches the crab. Even though the dummy is moving with constant speed, as it gets closer to the crab, the perceived angular speed increases. A certain threshold speed triggers a home-run. After reaching the burrow, the crab sits and waits while the dummy approaches and at some stage decides to enter the burrow. After having been underground for a while the crab resurfaces. Often, this happens while the
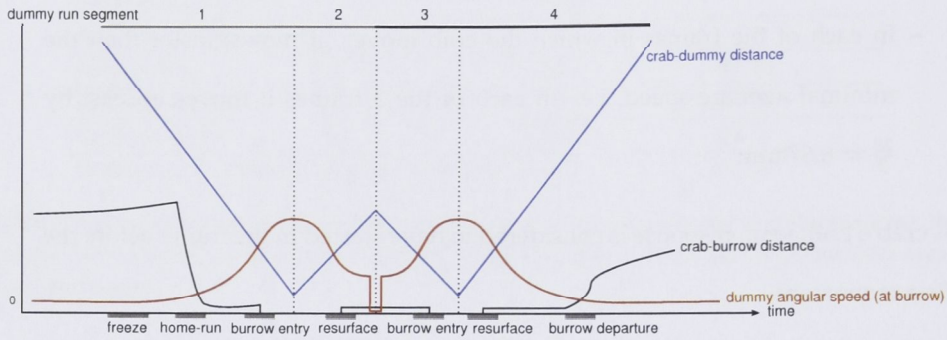
Figure 3.3: Schematic drawing of data collected for one crab. Shown are time series for crab-dummy distance, dummy angular speed and crab-burrow distance. The segments referenced are further defined in section 5.1. The black and grey bar mark the forward and backward movement of the crab.
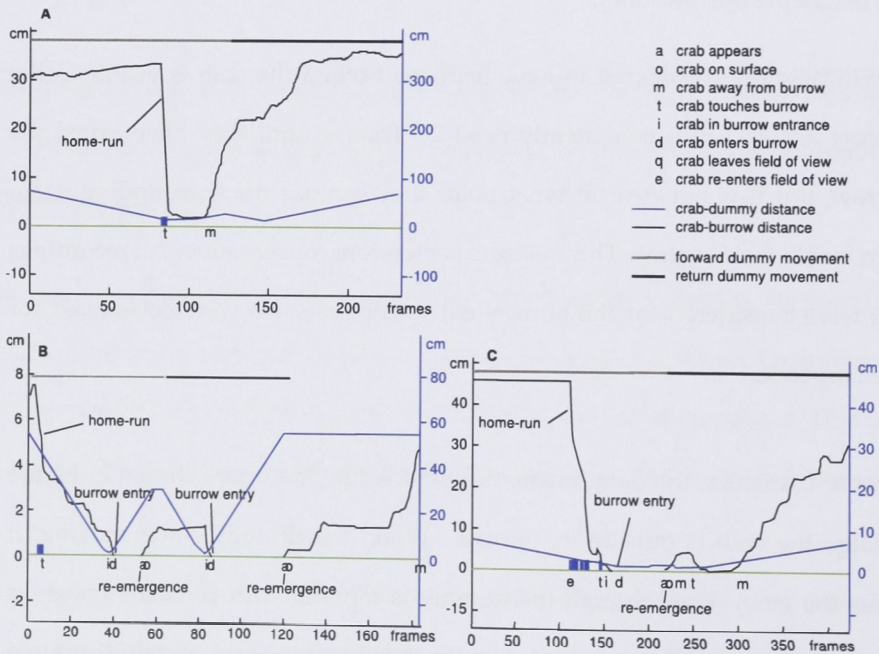
Figure 3.4: Extracted data for 3 runs. The crab-dummy distance is plotted along the x-axis. The blue rectangles show in which frames a home-run is detected. Transitions in behaviour categories are visualised by letters.

dummy is still moving but has passed the burrow so the crab-dummy distance is increasing. After resurfacing crabs do not move away from their burrow immediately, but stay and wait for a moment. Once the dummy changes direction and moves back, it approaches the crab again. On the way back, crabs often respond a second time by entering their burrow. The dummy is far away and keeps moving away as the crab is re-surfacing the second time. So the crab leaves its burrow and resumes feeding.

Figure 3.4 shows three examples of recorded crab reactions. In figure 3.4A, the crab reacts to the incoming dummy and runs home. Having made contact with the burrow, the crab waits and as soon as the dummy reverses, the crab moves away from the burrow again, resuming foraging. In figure 3.4B, the crab responds and runs home. At home it enters the the burrow immediately. After a short while it resurfaces and waits at the burrow entrance. Once the dummy returns, the crab goes underground again and resurfaces at the end of the dummy movement. It spends about 10-15 seconds (50-60 frames) at the burrow entrance before leaving the burrow to forage again. In the third sequence in figure 3.4C, the crab is initially out of view. It runs home and immediately enters its burrow. After resurfacing shortly before the dummy turns around it leaves the burrow and runs home a second time when the dummy comes close on the return movement. After the dummy has passed through the crab departs from the burrow. All three reactions are valid home-run sequences. Only the first burrow entry reactions in 3.4B and 3.4C are included in the analysis of burrow entry, as well as the respective emergence times.

Non-Linear Time Series Analysis - Clustering Analysis

Crabs gather information about the environment while they are responding to a predator. For optimal decision making, it would make sense to use information gathered during a response as basis for further decision making. For the analysis of such a response, this means that perception and behaviour during an early part of the response likely has an influence on the later response stages. Trying to analyse responses in separate stages may therefore be inadequate or require compensation for earlier behaviour to understand later decision criteria.

For a number of reasons it is difficult to actively model all possible interactions between subsequent measurements using a statistical analysis. These measurements are often correlated and through that cause problems with the stability of a statistical analysis. However, one can try to break up the response sequence into subparts based on the actual data not guided by external classifications and behaviour hypotheses. As consecutive observations are very redundant, this approach requires to summarise parts of each observation sequence and conglomerate them into clusters. Decision processes could then be modelled by transitions between these clusters.

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Ideally, the clusters determined based on the actual measured data should be consistent with the externally assumed decision structure - i.e. the behavioural stages described in chapter 1 should be reflected in the clustering structure, if the clustering works correctly and the assumptions about these stages were correct.

The outcome classifies the data in two ways. Firstly, decisions determined by the clustering describes a decision structure for all data traces, secondly the sequence of decisions for an individual trace describes what happened during a particular run.

Non-linear time series analysis often deals with systems whose current state is inferred from and influenced by previously measured variables. Therefore a formulation based on non-linear time series analysis would allow a description of the interdependency of subsequent decisions.

Once decision points and the temporal dependency structure are known, a statistical analysis can and should be employed, as it is a good tool to test correlations between variables in a verifiable manner.

I evaluated a clustering system that represents the recorded crab responses as a time series with multiple measurements at each point in time. Clustering was then done based on differences of measurement vectors and the history of the time series.

4.1   Methods based on Variable Space Clustering

Crab observations and the related reconstructed values are sampled at the same point in time. This allows us to combine all measurements at each point in time as a vector and those vectors can be combined into a multi-dimensional time series.

I considered the following variables for an analysis: crab-burrow distance, dummy angular speed and crab speed. The clustering can be easily extended to additional variables, however visualisation is hard for more than three variables and these variables should be enough to capture home-run response data.

All values measured and reconstructed for one crab during one movement of a dummy, in the following termed a run, can then be combined into a trace. This trace is running in the space spanned by the possible values of the measured variables (*variable space*). If the crab's deterministic behaviour is described by the measured values, all traces combined should occupy only parts of this space or the combined traces should have a specific structure. For instance, if crabs run home due to high dummy angular speed, there should not be any trace in the part of variable space with a high angular dummy speed and a large crab-burrow distance.

The so-defined time series consists of the sequence of measurements. In this way history information is encoded inherently in the data. Information about history effects such as an influence of early perceptions on later decision is therefore retained in this data formulation.

Data measurements refer to different physical entities. To cluster values in this space, a metric has to be chosen, which can compare two points in this variable space in a useful way, even if this metric has no direct interpretation in the physical world.

In order to identify structure and information in the variable space created from the crab observations in the way described, a time series clustering algorithm is used. It is described in section 4.2.

Non-linear time series analysis attempts to represent a high dimensional dynamic sys-

tem through a number of observed outputs of the system. In order to unambiguously describe the system state, the number of observations has to be sufficiently large. As not all states of the system can be measured, one employs a technique called time-delay embedding. Multiple observations of the system over time are combined into a vector providing a higher-dimensional representation of the system by including the history of the current system state. The number of time-delayed values needed for a sufficient representation of the system can be inferred from the dimensionality of the system's phase space [Takens 1981].

Crab behaviour is too high-dimensional for an unambiguous representation of its phase space following this technique. Especially as our recorded time series are short.

This leads to a problem known as *false neighbour problem* in chaos theory [Kennel et al. 1992]. When analysing a dynamical system, states close to each other in state space are expected to develop in similar ways in the future. When an attractor is mapped into a space that is of lower dimension than the required embedding dimension, it may intersect with itself. Usually, these points are detected by increasing the embedding dimension. When increasing the embedding dimension, points on similar parts of the attractor (real neighbours) should stay close to each other, while false neighbours will separate.

The clustering system has to be able to deal with a projection of different system states to the same measured vector-value. If the employed algorithm detects a false-neighbour pair of observations, it resolves this issue by locally discriminating members of this pair through additional historical information. This acts as if the delay-vector length was increased and for a small part of the reconstructed space it increases the dimensionality of the underlying modelling algorithm.

4.2 Algorithm Design

The clustering algorithm I used is a modification of the real-time dynamic systems modelling algorithm, presented in [Webers and Zimmer 2005]. My algorithm uses a different cell history definition, which simplifies cell splitting. It also does not include statistics about the time spent traversing an edge and no prediction method has been implemented. There is no inherent problem preventing this implementation in my algorithm, but it was not needed.

To facilitate the understanding of the proposed algorithm, a short overview is given below. Parameters relevant for the performance of the algorithm are described in section 4.2.1. A more detailed description of the algorithm is found in section 4.2.2. Finally a complete specification is given in section 4.2.3.

The clustering algorithm works on-line, processing one sample at a time. The general idea is to represent time series in form of a network structure, whose cells represent a vector of values in variable space connected by edges. One cell is considered to be closest to the last seen sample and called the best-matching or active cell. This closeness depends on the spatial position of the cell (a metric property) and the sequence of activations preceding this cell (topological information). A directed edge between two cells represents the fact that one was active right before the other one was active.

Subsequently, when encountering new samples, the active cell is re-determined. If an existing cell can be used as a new best-matching cell, this cell, and neighbours are adapted to match the current sample a little bit better. If no cell is in the vicinity of the new sample, a new cell is created at the position of the sample. If the new active cell is

not yet connected to the last active cell, an edge is introduced between the last active and the current active cell.

The clustering algorithm has the possibility to split a cell, if a false-neighbour problem is detected by checking the consistency of edges leaving a cell and thus makes sure that cells have a common ancestry.

4.2.1 Adaptation Parameters

The clustering system is controlled by a number of parameters:

- ρ - the *network granularity*. The larger this value is, the more vectors will be considered metrically close to a cell.

- s - the *topological granularity*. The topological radius (measured in number of transitions) in which adaptation occurs. This determines how locally adaptation is applied.

- α - the cell initial and maximal *adaptation rate*. This value is reduced with every sample the cell is adapted to and increased, if new cells are introduced in the neighbourhood of this cell.

- h_α - *adaptation half time*. This parameter determines after how many samples the cell's adaptation rate is halved.

- λ - a parameter determining the *power of the adaptation law*. This is 1 during all experiments

- *n* - the *trace length* determines how many cells are kept in the trace which is used to compare cell histories. Surprisingly, this does not seem to have a large influence on the resulting graph and is kept to be 1 or 2.

4.2.2 Algorithm Description

Initially, the clustering starts with an empty network. It then processes one sample at a time and adapts the corresponding network on-line.

Upon encountering a sample the network can be changed in the following ways:

- If no cell is found in the vicinity of the given sample, a new cell is created at the position of the current sample and connected to the previous best match via an edge. (*Adding a Cell*)

- If the trace follows a previously known pathway - the best-matching cell has not changed compared to the last sample or the transition happened along a known edge, all cells in the vicinity of the new current sample are adapted as follows: cells, which are close in variable space and have a similar history, are moved towards the current sample. This adaptation is slowed down over time to make the network converge eventually. (*Adaptation of Cells*)

- If the trace runs along a yet unknown path, but is in the spatial vicinity of an existing cell, a new edge is inserted from the previously activated cell to the new closest cell.

  However, the algorithm makes sure, that cells have only compatible outgoing edges with common ancestry, i.e. the traces leading out of a certain cell need to come from the same cell somewhere in the recent past. If an edge introduced

into the network is incompatible to the edges leaving its predecessor cell, this predecessor will be split. (*Cell Splitting*)

4.2.3   More formal specification

A Network N_t at any point in time t is a collection of a set of cells C_t, a set of edges E_t, a currently best-matching cell $b_t \in C_t$ and a trace T_t, i.e. a vector of the last n best-matching cells $T = (b_{i-n}, \dots, b_{i-1})$.

A cell c_i is a collection of its representation vector in variable space r_i and a history $H_{c_i} = \{c_j\}$, where H_{c_i} denotes the set of recently active cells before reaching c_i, and a cell-specific adaptation parameter α_i.

An edge e_i is a vector $\langle c_j, c_k \rangle$, $c_j, c_k \in C_t$ connecting two edges. For convenience let $H_{e_i} = H_{c_j}$, i.e. the history of an edge be the history of the cell it is originating from.

There exists a path $p(c_j, c_k)$ between cells c_j and c_k, if and only if there exists a set of edges connecting the cells via intermediate cells. The topological path length $|p|$ is defined as the number of edges $e_i = \langle c_i, c_{i+1} \rangle, i = 1 \dots |p|$ needed to traverse from c_j to c_k. The metrical path length $|p|_m = \sum_{i=1}^{|p|} |r_i - r_{i+1}|$ is the sum of distances between the nodes connected via e_i.

Then $comp(e_j, e_k)$ can be defined as a function denoting compatibility of edges

$$comp(e_j, e_k) = \begin{array}{ll} 1, & |H_{e_j} \cap H_{e_k}| \neq 0 \\ 0, & |H_{e_j} \cap H_{e_k}| = 0 \end{array}$$

Let the topological distance δ_t between a trace T_t and a specific cell c_i be

$$\delta_t(T_t, c_i) = -\sum_{c_j \in T_t} \begin{pmatrix} 1, & c_j \in H_{c_i} \vee c_j = c_i \\ 0, & otherwise \end{pmatrix}$$

When comparing T_t with b_t, the trace will contain b_t, however, b_t will not be in H_{b_t}. Therefore $\delta_t(T_t, c_i)$ should be increased by one, if the last cell in $T_t = c_i$.

Note that this distance is non-positive. As it will only be used to order cells, no normalisation as such is needed.

Given a new sample ζ_{t+1}, a network N_{t+1} can be calculated as follows:

1. Calculate the metric neighbourhood M of ζ_{t+1}.

$$M = \{c_i \in C_t \,||r_i - \zeta_{t+1}| < \rho\}$$

2. If $|M| = 0$:

   - create a new cell c_k, $r_k = \zeta_{t+1}$
   - $C_{t+1} = C_t \cup \{c_{t+1}\}$
   - $E_{t+1} = E_t \cup \{\langle b_t, c_k \rangle\}$
   - $b_{t+1} = c_k$.

   else:

   - $b_{t+1} = \{c_i \in M | \delta_t(T_t, c_i) \text{ minimal}\}$
   - if $b_t \neq b_{t+1}$, $E_{t+1} = E_t \cup \{\langle b_t, b_{t+1} \rangle\}$
   - if $b_t \neq b_{t+1}$, $H_{b_t} = H_{b_t} \cup (T_t \setminus \{b_t\})$, i.e. update the history of the cell when leaving the cell by adding all cells from the trace to the history of the cell except for itself.

- $C_{t+1} = C_t$, if all edges leaving b_t are compatible. Otherwise: Perform cell-splitting.

3. Finally adapt cells as follows:

- calculate the topological neighbourhood

$$P = \{c_i \in C_t | \exists p(c_i, b_t) \| p \| < s\} \cup \{c_t \in C_t | \exists p(b_t, c_i) \| p \| < s\}$$

Order this path by the metric path lengths.

If the network did not change in structure (no cells or edges were added with the last sample):

Adapt the cell centres according to their rank k in this ordered set:

$$r_{i,t+1} = r_i + e^{-\frac{k}{\lambda}} \alpha_{i,t} \left(\zeta_t + 1 - r_{i,t} \right)$$

Also adapt the cell-specific α as follows:

$$\alpha_{i,t+1} = \alpha_{i,t} \left(1 - e^{-\frac{k}{\lambda}} \left(1 - (1/2)^{\frac{1}{n_\alpha}} \right) \right)$$

Otherwise: for all cells c_i in P, increase their alpha values α_i according to their rank k as follows:

$$\alpha_{i,t+1} = \alpha_{i,t} + (\alpha - \alpha_{i,t}) e^{-\frac{k}{4\lambda}}$$

Cell-Splitting

Cell-Splitting is performed as follows: Given network N_t, and cells b_{t-1}, b_t through the trace and b_{t+1}, we have to split cell b_t:

1. create new cell c_{new}, with the same centre as b_t

2. $H_{c_{new}} = T_t \setminus \{b_t\}$

3. $E_{t+1} = E_t \cup \{\langle b_{t-1}, c_{new}\rangle, \langle c_{new}, b_{t+1}\rangle\} \setminus \{\langle b_{t-1}, b_t\rangle\}$

4. change trace, s.t. c_{new} replaces b_t.

4.2.4 Analysis Setup

As the network state and structure changes during the course of adaptation, it cannot be expected to have reached a steady state when the end of the dataset has been processed just once. Therefore it is necessary to repeat the analysis of a dataset until the network has converged. Convergence can be measured in two ways: firstly the structure of the network should not change when clustering the data again, i.e. no new cell should be added or removed; secondly the cell centres themselves should not move either. The first criterion is always achieved before the second is fulfilled, as newly inserted cells start out with a high adaptation rate α. To monitor the cell adaptation criterion, the sum of the absolute values of cell shifts is recorded. This value is measured in the used metric and usually has no dimension. The dataset is repetitively fed into the clustering algorithm and the number of repetitions increased, if the total adaptation in the last run is too high. The acceptance threshold depends on the number of samples in the dataset, as adaptation happens when processing each individual sample.

If the network model captures the underlying decision structure in a meaningful way, it should be robust to changes in network granularity. For instance, the underlying network structure should not change greatly when the resolution is varied. Of course

in clustering results with different granularity, paths in the network may be fused, but if significant changes in path layout occur, they can be considered artifacts of the modelling process.

It would probably be better to randomise the sequence in which time series are fed into the network. Randomisation would safeguard against a dependence of network structure on adaptation sequence, but the likelihood of these artifacts should be low. The topological differences which may occur due to a different sequence of time series processed should be irrelevant to the later interpretation. Therefore this was not implemented.

In addition to the raw structure of the network, it is interesting to gain statistics on the occurrence of transitions between cells. This can also be used to identify outlier data - for instance a route that has only been traversed by one trace while all other traces ran through a different route is probably an outlier.

The traces used for clustering have a restricted length and are reduced to stop before the dummy moves back. Therefore traces are not periodic, but the end cell of the trace is of interest as this cell should tell us what kind of response occurred. The starting point of a trace should be recorded to foster an understanding on how the trace is clustered in the network. Hence for analysis it is interesting to record, where a trace started and where it ended. Therefore, the number of traces starting in each cell are counted as the source value and the traces ending in each cell are recorded as the sink value of each cell.

As the sequence of cells activated by a specific time series may change due to adaptation, only statistics gathered from the last repetition are actually valid. Therefore,

after performing all repetitions necessary to stabilise the network, all counters are reset to zero and one test run is performed. This statistic for the test run is then used to produce the graph output.

The graph display (e.g. figure 4.3A) encodes this information as follows: Cells which are sources are placed to the left of the graph, sinks are placed to the right of the graph, normal cells appear in between. To control for outlier data, cells whose source count is less than the number of in-transitions (so more traces ran through this cell than originated in it) and cells whose number of out-transitions is more than the sink count are considered normal cells in terms of placement. Edge widths represent transition count, in addition, edges contain a numeric label showing the transition count.

4.2.5 Metric

The metric employed is the Euclidean distance of the vectors formed by scaled input variables. This metric has no physical correspondence, however small changes in variables will reflect small changes in perceived state.

Scaling is performed as follows:

- *Crab-burrow* distance is normalised based on each individual run, such that the starting value corresponds to 1, if the crab is more than 50mm away from the burrow at the start of the experiment. If the crab is initially closer, it is considered to be home and all crab-burrow distance values are set to 0.

- *Dummy elevation*, *dummy angular speed* and the *horizontal* and *vertical dummy velocity* components are scaled by the same factors for the whole set to make all values lie between 0 and 1.

- *Crabspeed* was not scaled, but measured in units of crabspeed, i.e. consecutive differences between crab-burrow distance. Hence the values were in the same orders of magnitude as crab-burrow distance.

4.3   Results

4.3.1   Modelling System Testing
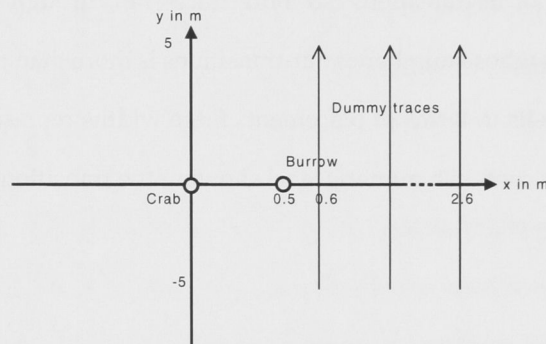
Figure 4.1: Setup of virtual crab simulator. The crab starts at the origin, the burrow is on the X-Axis at 0.5m distance. The dummy runs along transects that are uniformly distributed at a distance from the crab between 0.6m and 2.6m. The dummy moves from y=-5m to y=5m with a speed of 0.2 m/s.

To test whether the clustering system is in principle capable of extracting decision processes and to aid in interpretation of the network structures obtained from real data, a virtual crab simulator was developed to create data in the same coordinate frame and format. However, the decision process was known and the noise level controllable. The simulator can thus be used to distinguish modelling results caused by decision processes from structures which are introduced by the pure geometrical setup of the experiments.

The setup of the simulation experiments is shown in figure 4.1. The crab sits at the origin with the burrow being 0.5m away on the x axis. The dummy moves always

parallel to the y axis at different distances from the crab with fixed speed. The crab "observes" the dummy and as soon as the angular velocity of the dummy at the crab's position exceeds a given threshold, the crab runs home. If the threshold is never exceeded, the crab will not move. To study the influence of changing decision parameters on the final clustering network, the crab's decision threshold is drawn from a Gaussian distribution (mean $10 \pm 2°/s$).

The result of 30 such runs projected into a coordinate system consisting of the axes Crab-Burrow DISTance (CBDIST), Dummy Angular SPEED (DASPEED) and CRAB SPEED (CRABSPEED) is shown in figure 4.2A. In addition, the data were also plotted with a time axis in figure 4.2B to allow a better understanding of the temporal characteristics of the data.

As these figures are the output of the clustering process, CRAB SPEED was normalised as described in section 4.2.5, however the initial Crab-Burrow DISTance was the same in all test runs (0.5m) and therefore not scaled.

All traces in figure 4.2B start at time 0, DASPEED 0 and CBDIST 0.5. With the progression of time, the dummy starts moving while the crab sits still. Gradually, DASPEED increases. If the crab responds and decides to run home, the trace will branch forward (towards CBDIST 0). Once the crab has reached that point, it will sit still but the dummy is still coming closer, causing a further increase in dummy angular speed. Once the dummy has passed its closest point to the crab, the dummy speed will decrease towards the right hand of the graph. If the crab does not react, CBDIST will be constant and the trace will remain in the back of the graph, nevertheless showing an increase and decrease in dummy speed.

Figure 4.2A shows the same traces in a different projection. Instead of a time axis, CRABSPEED is plotted. This is the variable space in which clustering is done. Traces start at CBDIST 0.5, DASPEED 0 and CRABSPEED 0. When the dummy approaches, DASPEED will increase. If the crab does not respond, the reduction of dummy angular speed after it has passed the crab will make the trace return onto itself and finish in the same corner. If the crab does react, it will start moving, causing a high CRABSPEED value. While the crab is running home, CBDIST gets smaller until it reaches 0. At this point, the crab stops moving, so CRABSPEED goes back to 0 too. The crab is home before the dummy has reached its closest point, which means after the crab stopped moving, DASPEED increases and then decreases.

The shown data were clustered using the following parameters: network granularity $\rho = 0.2$, adaptation half time $h_\alpha = 1.0$, initial adaptation rate $\alpha_{initial} = 0.1$, topological granularity $s = 2$. Due to the missing noise in the data, the adaptation halftime h_α could be kept low and still fit the data appropriately. The red circles in figure 4.2A represent the centres of the cells placed. Please note that the cells actually have a radius of size 0.2, i.e. they are usually touching or even intersecting.

When analysing figure 4.2B with respect to the clustering result, it is important to keep in mind that time is not actually used in the distance metric of the clustering system and the time at which cells are plotted represents the time at which this cell was created. Therefore the time axis helps to understand the time series, but is misleading when analysing the clustering results.

Figure 4.3A shows the network graph obtained from this sequence. This network model encodes that traces leaving the cell on the origin (cell 0) will go through a sequence of cells with high crab speed and similar other parameters. While
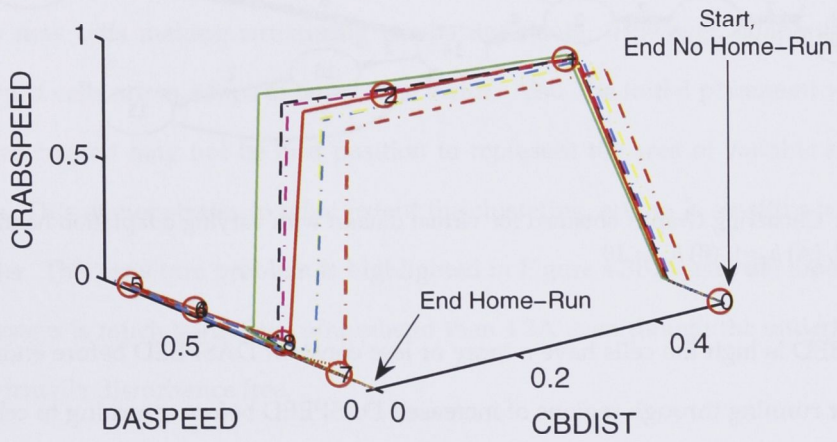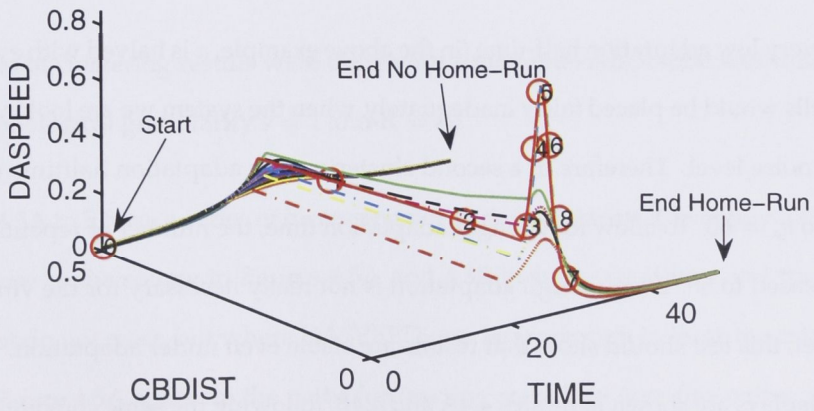
Figure 4.2: Time traces created by virtual crab simulator and cell positions for clustering with low adaptation halftime ($h_\alpha = 1$)
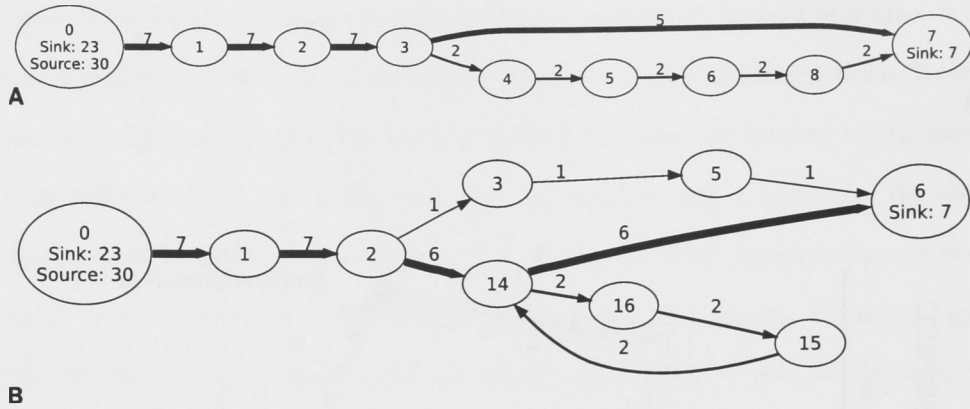
Figure 4.3: Clustering Graphs obtained for virtual dataset with varying adaptation halftime h_α. $\rho = 0.2$, (A) $h_\alpha = 1$, (B) $h_\alpha = 10$

CRABSPEED is high the cells have a more or less constant DASPEED before ending in cell 7 or running through regions of increased DASPEED before returning to cell 7. The actual decision point is happening in cell 0 only. The network granularity is so large, that no cell other than 0 is generated for speeds that did not cause a home-run response. This means, the decision whether a crab runs home or not is given by the fact whether a trace ever leaves cell 0.

By using a very low adaptation half-time (in the above example, α is halved with every sample), cells would be placed fairly inadequately, when the system we are looking at has a high noise level. Therefore in a second clustering, the adaptation halftime was increased to $h_\alpha = 60$. To allow for a longer adaptation time, the number of repetitions is also increased to 60. Even though adaptation is not really necessary for the virtual crab data set, this test should show that results are stable even under adaptation. The resulting displays are shown in figures 4.4A and 4.4B, following the same conventions as above. The resulting graph is shown in figure 4.3B.

The choice of the adaptation half-time presents a first problem. By allowing cells to

shift in order to adapt to consecutive samples, they tend to get dragged along the time series. This means, if the time series is changing at the wrong speed, cells get moved away from their original position and when a similar time series reaches this part of space again, this cell cannot match the new time series. This leads to the creation of many new cells making structuring results unreliable. However, adaptation is necessary, if cells are to adapt to noisy time series. Also, the initial placement when a cell was created may not be best position to represent the area of variable space it covers. This demonstrates to what extent the clustering system is sensitive to this parameter. This structure problem is highlighted in Figure 4.3B, where the topology of the system is much harder to comprehend than 4.3A even though the underlying data is virtually disturbance free.

To make sure that the modelling outcome is actually robust, a series of clustering runs was performed with different smaller network granularities ρ. This procedure also illustrates the effect of paths merging slowly when the granularity of the network is increased.

The series of clustering results were done with a moderate adaptation half-time $h_\alpha = 10$, the topological granularity $s = 1$ and $R = 20$.

Figures 4.5A to E form a series of increasing network granularity. The highly traversed edges close to the source in figures 4.5A and 4.5B include transitions and traces for crabs that do not react, but where DASPEED gets large enough to leave the cell at the origin. Figure 4.5A splits up the paths for reacting crabs into very fine paths, at most 2 traces traverse the same path during their peak. in Figure 4.5C, some of these paths merge and there are only three different paths around the peak DASPEED (through cells 19, 5 and 15 respectively). In Figure 4.5C, the three paths through the peak still
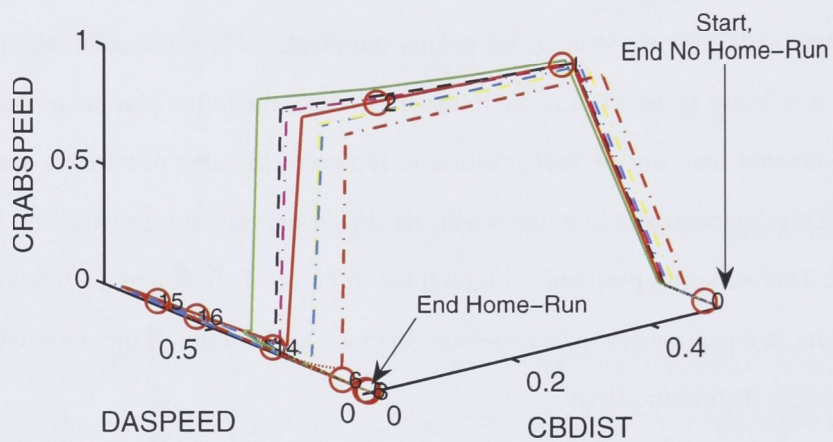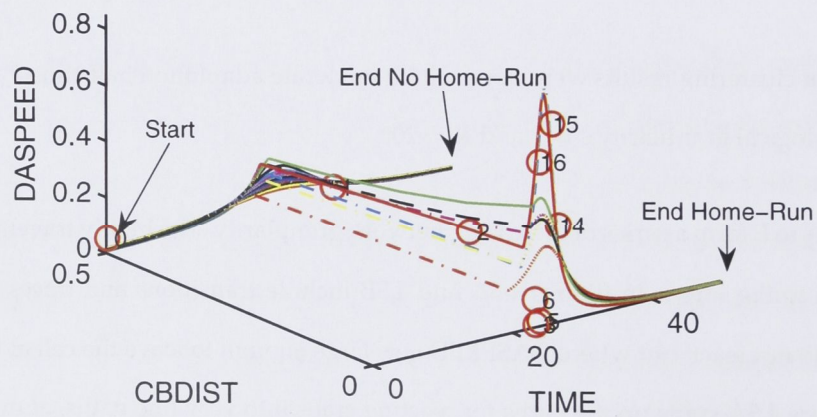
Figure 4.4: Time series data and network cells for clustering of virtual crab data. Network granularity $\rho = 0.2$, adaptation half-time $h_\alpha = 10$, repetitions $R = 20$

exist, but several cells on the way have merged, so that the number of transitions for each trace is smaller. In figure 4.5D paths have merged, such that three paths exist through the network, all ending in just one sink. These paths shorten by another cell in figure 4.5E.

In figure 4.5B, for some non-reactions, the dummy angular speed was high enough to leave the source cell. These cells connect to another sink cell 1.

Figure 4.5C shows that the clustering result can be sensitive to network granularity. The region for the end of the home runs actually is covered by several cells with similar positions. These cells were created during the adaptation phase, while the main sink cell was out of the way. Once such a path has been established it is unlikely that it will be removed while the network is settling down.

Figures 4.5B, D and E display another problem with the clustering result. Even though the traces have no repetitive dynamical properties, the clustering graph includes a cycle (from cell 3 to 7 and back and from cell 12 to 17).

Apart from the wrongly backwards pointing edge, the clustering graphs are more or less consistent for different granularities. All paths start at the same source cell. Increasing dummy angular speed or an increase in CRABSPEED due to a reaction forces the trace to leave the source cell. Home-runs traverse a region of high CRABSPEED while CBDIST goes to 0. At this point there is some kind of peak in dummy angular speed that is often modelled by several different paths.

However, most of the network structure is used to describe dynamical properties due to the geometrical setup. In most graphs, only cell 0 and the edges leaving it are related to the decision process. Also, branching points exist in all graphs consistently
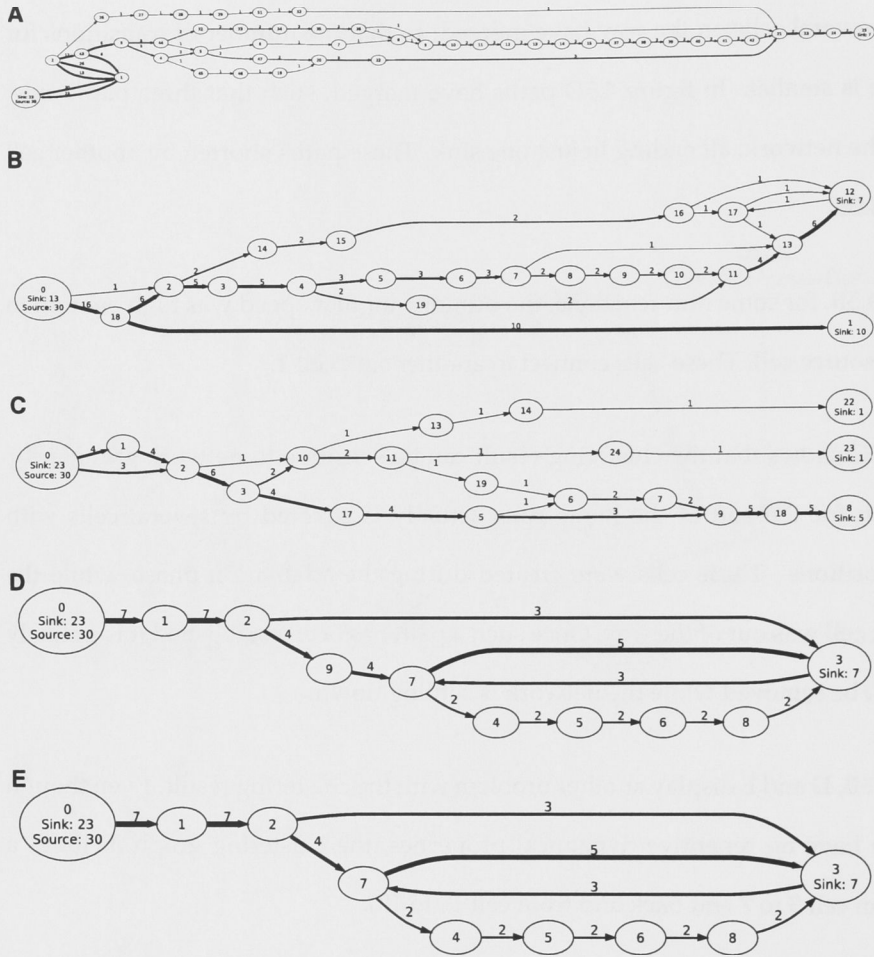
Figure 4.5: Clustering graphs for virtual crab data for varying network granularities. (A) $\rho = 0.05$, (B) $\rho = 0.10$, (C) $\rho = 0.15$, (D) $\rho = 0.18$, (E) $\rho = 0.20$.

not only at the actual decision point but elsewhere in the graph. It is not easily possible

to deduct the modelled crab decision structure from the obtained graphs even in this

very simple case.

4.3.2 Data Set Selection for real data

Real-Life data were digitised from the recorded video files using Matlab and therefore time series are available as a Matlab data structure. Data were organised according to the date the recordings were taken and the camera used. There exists a unique identification string for the dataset recorded by one individual camera.

Data inside this set can be accessed according to crab individual and the respective run.

To ease analysis, real data from these runs were shortened to only include the approaching run of the dummy. This was done, because some crabs tend to interrupt their home-run as soon as the dummy stops moving and move away from the burrow again. Restricting the time series this way made all the end points of the time series come to lie very close to the minimal crab-burrow distance that occurred during the run. Therefore the end of the trace could give an idea about how strong the home-run response was.

4.3.3 Data Set Analysis

Datasets for analysis were formed from data collected for an individual crab. Trying to combine all data from a camera observation (10 crabs, 15 runs) into one dataset created a graph too big for interpretation.

Figure 4.6 shows clustering results for the runs of crab number 4. Adaptation parameters were as follows: granularity $\rho = 0.3$, adaptation half time $h_\alpha = 10$, repetitions $R = 20$. The dataset has 985 samples and total accumulated movement

at the end of repetitions was $2.50442 \cdot 10^{-04}$ (measured as sum of all movements in the last test run in the metric). This can serve as a good measure for convergence. On average, each sample caused a shift of cells of less than 10^{-6} in the last repetition. The network granularity was increased for this dataset in comparison to section 4.3.1 to keep the number of nodes in the resulting network manageable.

Traces in figure 4.6 now have two different starting points, depending on whether the crab was at the burrow during the beginning of the run or whether it was away from the burrow. Traces that start at the burrow will stay at a CBDIST of 0 due to the normalisation. They will experience an increase in dummy angular speed and a decrease during the run. All of these traces are in the line on the left hand side of figure 4.6A and in the foreground of figure 4.6B. Traces for crabs which are away from the burrow and do not react, will start on the right hand side of figure 4.6A or the background of figure 4.6B. They too undergo an increase of dummy angular speed. Some crabs move a little during the run but do not display an actual home-run decision. Three traces can be seen to represent a home-run response. The yellow and black traces are traces of a full home-run, running from the right hand side of figure 4.6A to the left. The cyan coloured trace ending in cell 12 is a partial home-run. The blue trace that seems to run towards the front of figure 4.6B is a projection artifact. When comparing the trace with its plot in figure 4.6A, it is obvious that the trace does not constitute a home-run.

In contrast to the artificial dataset from figure 4.4, one can note, that there is much more variation in the crabs "resting state". Even though crabs are not responding, their position shifts as they move around during their normal foraging activity.

In a first step to analyse the resulting clustering graph (figure 4.8B), the respective

source and sink nodes can be grouped. Due to the scaling applied, all traces start in either of two possible states: the crab is out of the burrow or it is at or in the burrow entrance while the dummy angular speed is still 0. Cell 0 represents runs, where the crab started outside of the burrow, cell 2, where the crab was at the burrow. Sinks can be sorted in a similar way: cells 0 and 11 have a high crab-burrow distance component, which means traces ending there are from dummy runs where the crab shows no or only a weak response. Cell 10 is in the middle, but it is not clear, whether this represents a reaction or is due to the large radius of cells. Finally, cells 1, 2, 5, 19 represent a response that ended close to the burrow. Traces ending here can be a home-run reaction or, if the trace started close to the burrow, the trace would represent a crab waiting at the burrow.

It is interesting to look at traces which come from a high crab-burrow distance and end in the burrow, as they are actually reactions. Two clear transitions can be observed, namely one via cell 9 and 10 and one transition via cell 7. Both of these cell traces run through regions with high dummy angular speed.

It would be informative to have a list of cells visited for all traces through the network, as this might help the interpretation. Unfortunately, this cell trace is not recorded in the current implementation.

Figure 4.7 shows the same result for an adaptation half-time $h_\alpha = 1.0$. The repetitions $R = 10$ could be reduced as adaptation happened faster (movement in last run was $2.44141 \cdot 10^{-08}$). The resulting graph (4.8A) is very similar with respect to the response sequences. Cell 0 is the starting point for traces away from the burrow, cell 2 the starting point for close traces. Cells 0 and 6 are end points for no reactions, cell 1 is the end point of a partial home-run, cell 2 is a sink for full home-runs or for crabs not

leaving the burrow. Cells 8 and 9, 10 are on paths of a complete home-run.

4.3.4   Discussion

The results of NLTSA of this data set are very unsatisfactory. The large number of nodes obtained and the very large number of branching points in the graphs make the interpretation of the results virtually impossible. Knowing the underlying decision model it is possible to trace back these decisions through the graphs. However it is impossible to deduce a model underlying the decision process from the final clustering network.

Even for the virtual dataset, figure 4.3A displays 1 branching point which actually does not represent the underlying decision model. Similarly, figure 4.3B displays 3 branching points unrelated to the actual decision. The second graph which analysed the most basic decision models available in the data format of our experiment also introduces a cycle.

Comparing these two figures also shows that the clustering result is likely to cause large problems when cells can adapt. Allowing for more adaptation further increases network complexity and adds false links. Comparing figures 4.7 and 4.6 highlights this problem. Through adaptation the network tends to become more complex, as cells shift forth and back and cells are created that lie on top of each other. During these shifts, new edges are introduced and seem to clutter the histories of existing cells causing a number misalignments and misleading edges.

As fusing cells caused most of the problems understanding the graph, a version of the clustering algorithm was produced that did not allow a new edge to be introduced

A
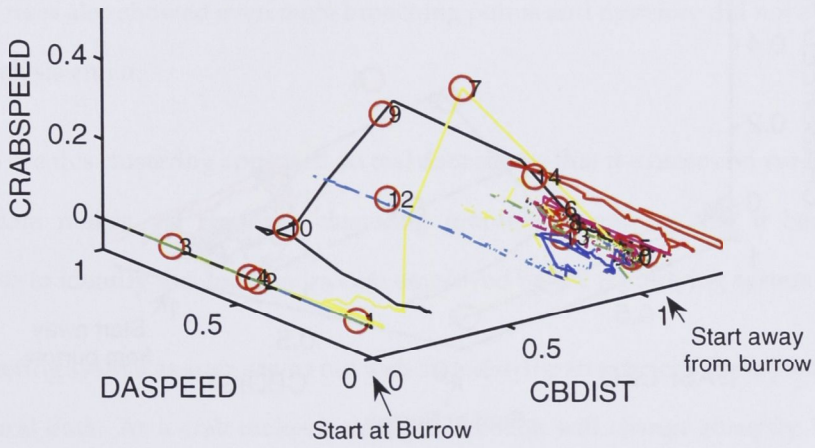
B
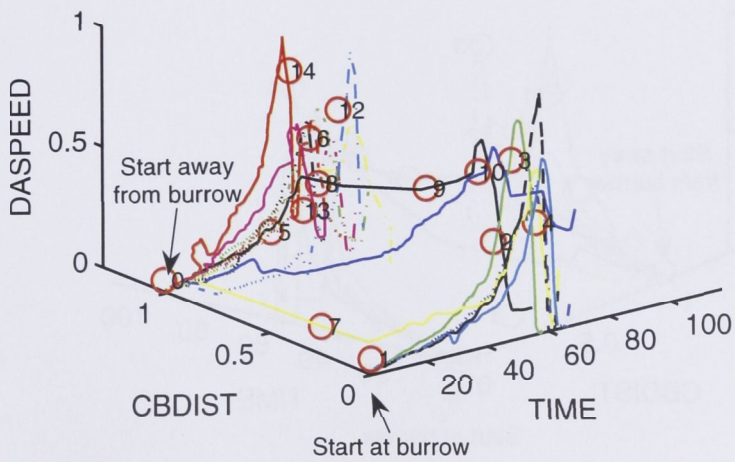
Figure 4.6: Time Series and Network Cell Positions for data from real crab. ($\rho = 0.3$, $h_\alpha = 10$, $R = 10$)

A
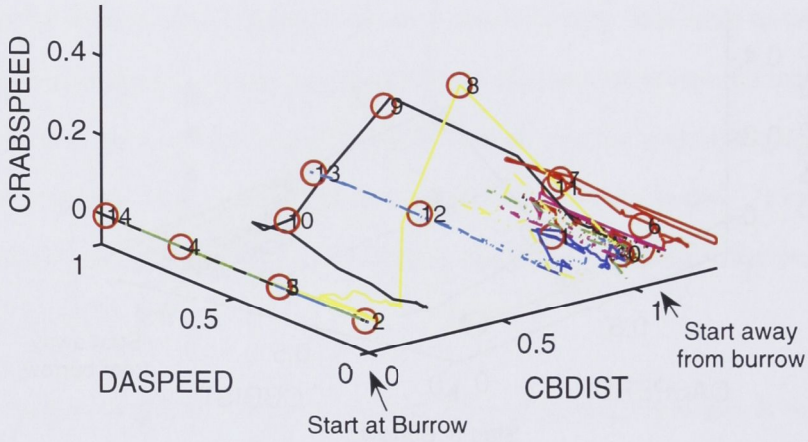
B
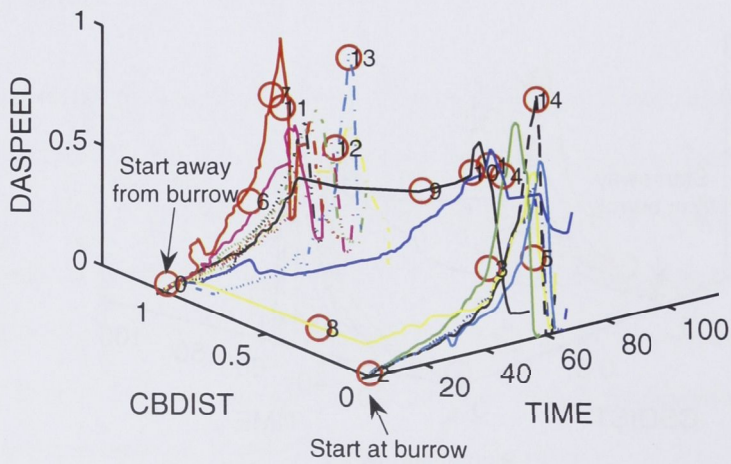
Figure 4.7: Time Series and Network Cell Positions for data from real crab ($\rho = 0.3$, $h_\alpha = 1$, $R = 10$)

into the network unless it connected to a newly created cell. As a result, the clustering graph would become a tree. This made interpreting the resulting graphs easier, as it was more intuitive to relate cells to actual traces, but it removed all modelling aspects from the algorithm, as this simply re-sampled the variable space using cells. The resulting trees also showed even more branching points and therefore did not allow a better analysis either.

Trying to use this clustering approach on real data shows that the noise and variability in real data makes the resulting clustering graphs so complex that it becomes impossible to identify the decision process employed by the underlying system.

The clustering system as such seems not well suited to the structure of these particular behavioural data. As a crab makes a decision, its state will change abruptly, but in between these decisions the dynamics are highly predictable. However, the clustering algorithm needs to devote a lot of resources into modelling the dynamic development between decisions and as such hides any discrete decision making events.
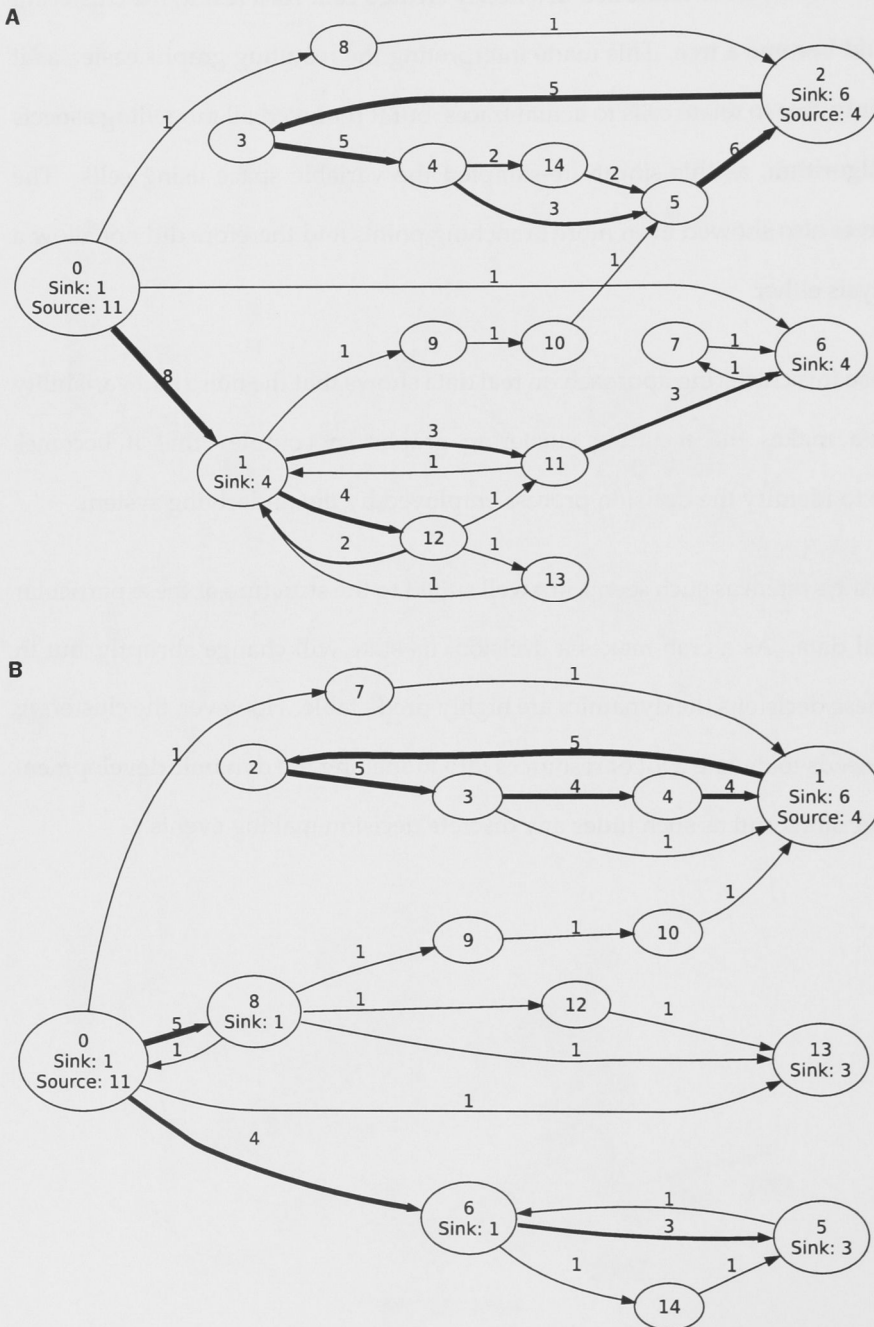
Figure 4.8: Clustering Graphs from real data. (A) no adaptation (corresponding to Figure 4.7), (B) adaptation (corresponding to Figure 4.6)

Statistical Analysis

The analysis using non-linear clustering methods proved to be ill-suited and failed to give insights into the decision process employed by crabs. A statistical analysis, however is still possible by sub-dividing the response sequence manually and modelling temporal interdependence explicitly.

In the following analysis of response timing and response cues, I will analyse the home-run stage, the burrow entry stage of the response and the burrow waiting time. Response cues for the home-run response will be analysed to compare results with those presented previously by [Hemmi 2005a; Hemmi 2005b].

For the statistical analysis a number of assumptions about the crab decision process have to be made. Decisions are assumed to happen just before transitions between the behavioural stages described in section 1. As dynamical changes in variables between the decision points are smooth and predictable, I assume that information immediately preceding the decision is sufficient to explain the respective decisions. In order to minimise influence of previous stages of the response, all decisions have to be similar with respect to those earlier stages. For instance, only home-run responses were included in the analysis when the crab is away from the burrow before the dummy started moving. Similarly, burrow entry responses are only included in the

analysis, if they were preceded by a home-run. The decision when to resurface has to rely on information that was gathered prior to this decision as the crab has lost any possibility to sense the predator while it is underground. Therefore the burrow wait time is analysed with respect to the visual information available at burrow entry.

In this experiment, the geometry of the dummy approach leads to a separation of visual cues into two groups. Because the height above ground and the size of the dummy were held constant, dummy elevation and the size of the dummy on the crab's retina is perfectly correlated to the distance between the crab and the dummy, while the retinal speed of the dummy and any dynamical cue such as the speed of expansion or time to contact are correlated with the speed of approach. So my analysis focuses on distinguishing these two kinds of cues.

The statistical analysis is made difficult by the fact that there is a strong correlation between crab-dummy distance and angular speed. Dummies that are closer to a crab will elicit higher angular speeds. The change of angular speed is highly non-linear with respect to crab-dummy distance. For large distances, changes are small, but when the dummy gets close to the crab, the angular speeds grows very quickly. This effect is stronger when the crabs are closer to the dummy rail.

5.1   Dummy Run Segmentation

With respect to risk imposed by a bird dummy, four sections can be distinguished in a dummy run (Figure 5.1). Initially, the dummy is approaching the crab until it reaches its closest point to the crab on the forward movement (section 1). It then continues to move past the crab (section 2). After reaching the end of the dummy rail, the dummy
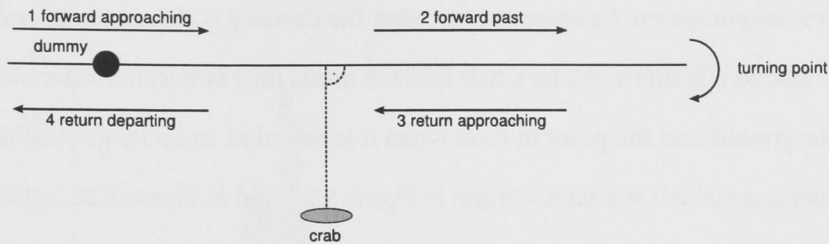
Figure 5.1: Different segments of a dummy run with respect to the closest point of approach to the crab

approaches the crab once again on the return movement (section 3) before passing it and departing (section 4). During the whole run, the dummy is visible to the crabs.

For reactions to conspecifics it can be shown, that crabs are more sensitive to a dummy that changed direction [Hemmi and Zeil 2003a]. It therefore can be expected that crabs also respond differently to a change in direction or to an approaching or retreating dummy bird.

Due to the individual crab position relative to the dummy rails and the different dummy speeds, each segment has a different length. However, it is still possible to align each individual run with respect to the transition points between segments.

Figure 5.2A shows the delay between the time a crab entered the burrow and the moment in time when the dummy is closest to the burrow (this is the transition from segment 1 to segment 2). Figures 5.2B and C show the time crabs entered the burrow with respect to the turning point (figure 5.2B, transition from segment 2 to 3) and the closest point of approach on the return movement (figure 5.2C, transition from segment 3 to 4) respectively.

In segment 1 most reactions happen before the dummy is at its closest point to the crab. The number of responses drops sharply around the time the dummy passes

the crab. A few responses can be observed just after the dummy is closest to the crab. This delay in reactions is due to the fact, that the crab needs time between the decision to move underground and the point in time when it is recorded as no longer visible. There is a small gap about 0.4s past the origin in Figure 5.2A and in Figure 5.2C, which show responses with respect to the closest approach of the dummy on the forward and return movements. The start of this gap is consistent with the time it takes most crabs to enter their burrow and disappear out of sight. I therefore assume for my analysis that the crab's reaction to enter the burrow is made 0.4 seconds before the crab has disappeared.

There is no such gap in figure 5.2B, which shows burrow entry responses with respect of the dummy turn around point, this is not expected either.

5.2   Mixed-Effect Model Design

In addition to describing an effect, it is desirable to calculate the probability of a dependency. This requires statistical modelling. Analysis of Variance (ANOVA) is a common and well-known method. However, for comparisons between groups, ANOVA requires groups to have the same size.

An analysis using mixed-effect models is similar to an analysis of variance approach, where the block structure is captured through random effects of the model. However, mixed-effect models are able to deal with unbalanced designs, i.e. designs with different group sizes.

For the crab dataset, a number of random factors describe the block structure. The top grouping factor is the session identity, within this, there are different camera
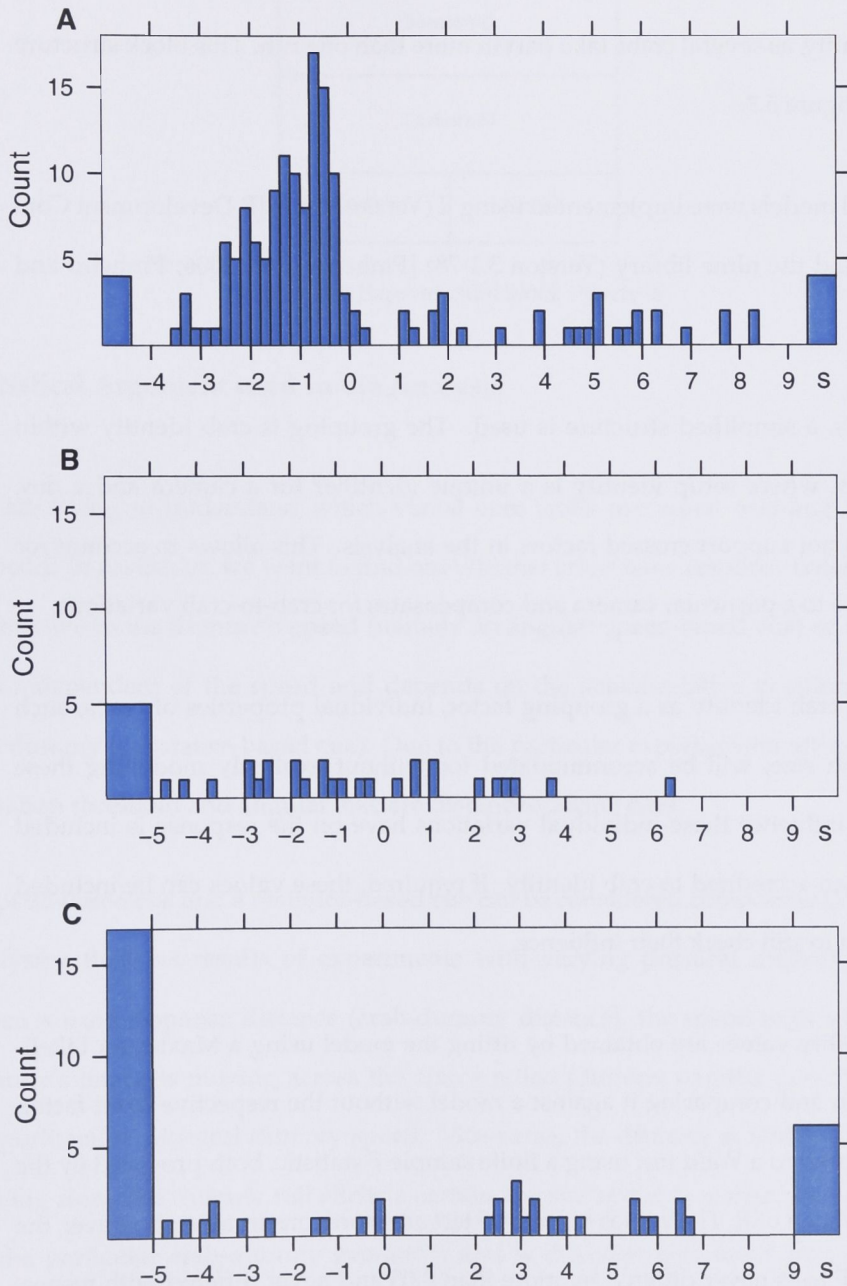
Figure 5.2: Burrow Entry times with respect to (A) the frame where the dummy is closest to the burrow on forward movement (responses from segments 1, 2, 3), (B) the frame where the dummy turns around (responses from segments 2, 3), (C) the frame where the dummy is closest to burrow on return movement (responses from segments 2, 3, 4).

sequences. Within each camera sequence there are two crossed factors, run number and crab identity, as several crabs take part in more than one run. This block structure is shown in Figure 5.3.

The statistical models were implemented using R (Version 2.4.1) [R Development Core Team 2006] and the nlme library (Version 3.1-78) [Pinheiro et al. 2006; Pinheiro and Bates 2000].

In the models, a simplified structure is used. The grouping is crab identity within setup identity, where setup identity is a unique identifier for a camera and a day, as nlme does not support crossed factors in the analysis. This allows to account for variations due to a particular camera and compensates for crab-to-crab variations.

By including crab identity as a grouping factor, individual properties of crabs, such as gender and size, will be accommodated for without explicitly modelling these factors. The influence these individual variations have on the response is included in the variation accredited to crab identity. If required, these values can be included in an analysis to still check their influence.

Cited probability values are obtained by fitting the model using a Maximum Likelihood criterion and comparing it against a model without the respective fixed factor. This is compared to a Wald test using a finite sample F statistic, both provided by the `anova()` function of R. The values from the F test are more conservative, however, the results from F tests never differed by more than 0.05 and never differed with respect to the 5% confidence level, unless otherwise indicated. Because for some models, an inspection of diagnostic plots for the models revealed problems, unclear models were also checked using a Kolmogorov-Smirnov test [Conover 1971, pp. 309-314].

SessionID	
CameraID	
CrabID	RunID
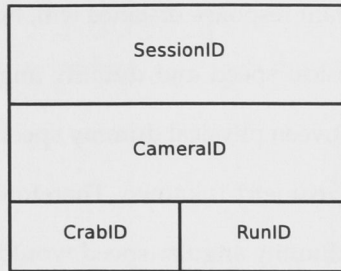
Figure 5.3: Experimental block structure

Statistical Argument used in the Analysis

We are trying to understand which visual cues crabs use when deciding when to respond. In particular, we want to find out whether crabs use a response criterion that is sensitive to the dummy's speed (namely an angular speed-based cue) or whether it is independent of the speed and depends on the actual relative position of crab and dummy (a distance-based cue). Due to the particular experimental setup, a fixed elevation threshold and angular size are distance-specific cues.

A speed-based cue and a distance-based cue can be considered complementary when analysing them as results of experiments with varying physical dummy speeds. Given a fixed response distance (crab-dummy distance), the speed with which the dummy's image is moving across the crab's retina (dummy angular speed) will be proportional to physical dummy speed. Vice-versa, the distance at which a dummy moving along the dummy rail elicits a certain angular speed is perfectly determined by the particular crab-dummy geometry, and is therefore correlated with, but not directly proportional to crab-dummy distance.

If crabs use distance as a decision criterion, response distance will be independent of physical dummy speed and the response distance and physical dummy speed will

therefore be uncorrelated. A constant response distance will, however, cause a strong correlation between dummy physical speed and dummy angular speed at time of response. The size of the effect between physical dummy speed and angular dummy speed is entirely predictable if the geometry is known. Therefore, to test the size of this effect, we can calculate what the dummy angular speed would have been, had all of the dummies moved with the same physical speed (see Appendix A.1). If this rescaled dummy angular speed were uncorrelated with physical speed, this would indicate that the crabs did not respond to the dummy's physical speed at all and would further support the claim of a distance-specific cue as basis for a response.

In a complementary way, if crabs use an angular speed-based cue, their angular speed will be constant regardless of physical dummy speed. Therefore the dummy's angular speed at time of response will be uncorrelated with dummy physical speed. Response distance however will be correlated with physical speed. The effect due to a fixed angular speed at the time of response on the correlation between physical dummy speed and response distance can be removed by rescaling the response distance to the distance at which a dummy moving with a fixed physical speed along its rail would have elicited the angular speed observed at the response (see Appendix A.2). If the rescaled response distance is independent of the dummy's physical speed, the decision must be based purely on angular speed.

5.3   The Home-run Response

The dummy angular speeds at which the crabs reacted are shown in figure 5.4C. The responses are split into three groups according to the dummy's physical speed. The
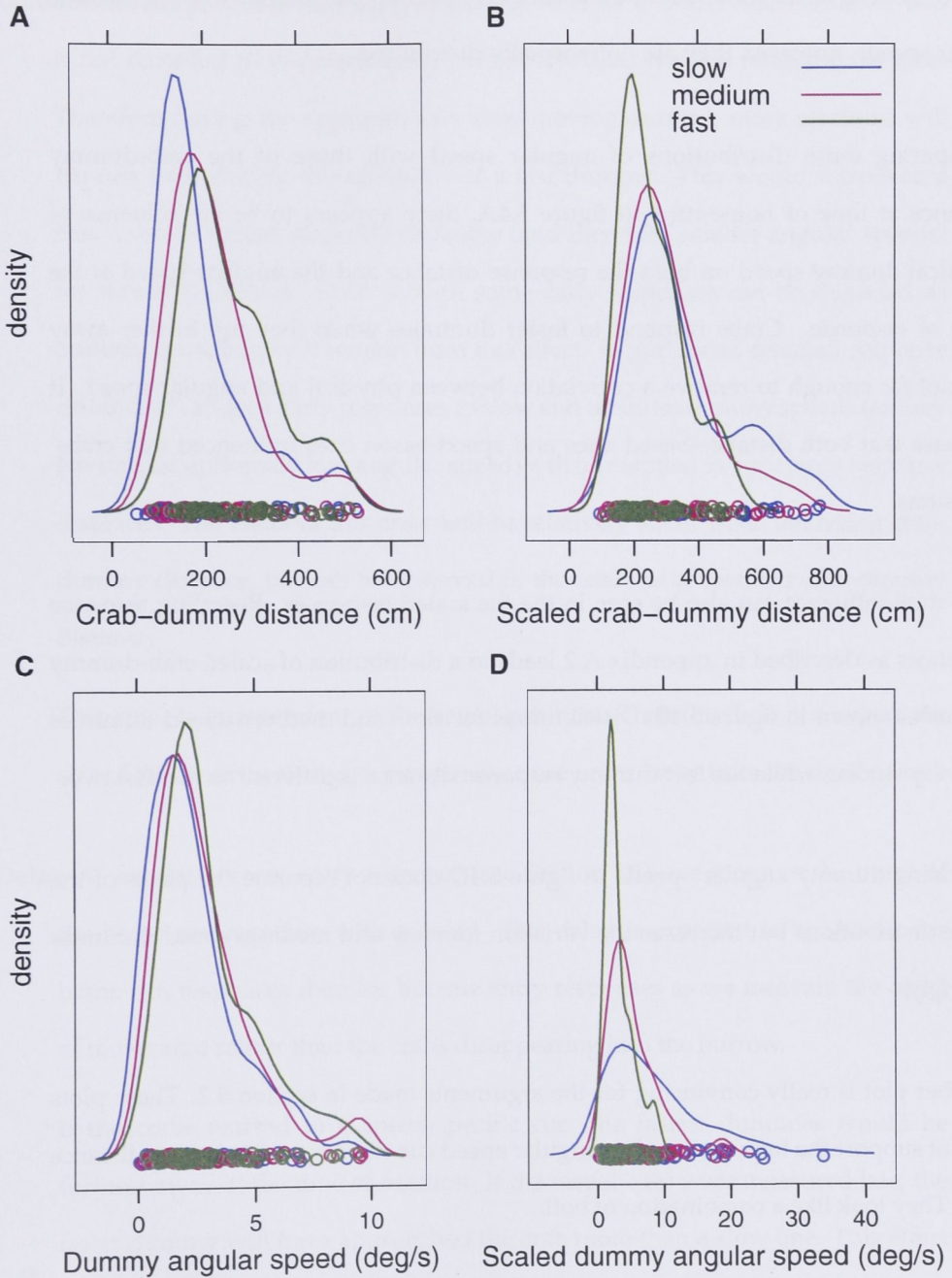
Figure 5.4: Visual Cues for Home-Run. (A) Crab-Dummy Distance, (B) Crab-Dummy distance that would have caused the observed angular speed had all dummies moved as fast as the fast dummy, (C) Dummy Angular Speed, (D) Dummy Angular Speed that would have been observed at the observed response distance, had all dummies moved as fast as the fast dummy

graph shows that the three distributions are very similar. Due to the large tail towards larger speeds, however, they are not normally distributed.

Comparing these distributions of angular speed with those of the crab-dummy distance at time of home-runs in figure 5.4A, there appears to be an influence of physical dummy speed on both the response distance and the angular speed at the time of response. Crabs respond to faster dummies when they are further away but not far enough to remove a correlation between physical and angular speed. It appears that both distance-based cues and speed-based cues influenced that crabs' decisions.

This dual influence can also be seen in the the scaled responses. Rescaling response distances as described in appendix A.2 leads to a distribution of scaled crab-dummy distances shown in figure 5.4B. Distributions for slow and medium speed dummies are very similar, while the fast dummy response distance is different to the first two.

Rescaling dummy angular speeds in figure 5.4D does not separate the peaks of the three distributions but increases the variation for slow and medium speed dummies strongly.

Neither plot is really convincing for the arguments made in section 5.2. These plots do not support the hypothesis of an angular speed cue nor a hypothesis for a distance cue. They look like a combination of both.

However, there are three potential error sources in the experiment that could have led to this result. These error sources introduce a consistent bias away from an angular speed cue towards a distance-based cue as discussed below.

Random Reactions Crabs may react randomly or react to some external factor that
is not recorded in the experiment. These reactions happen randomly in time.
Therefore during the approach of a slow moving dummy, more reactions will
happen than during the approach of a fast dummy. This would introduce a
bias towards longer response distances (and therefore smaller angular speeds)
for slower dummies. Even though some early responses can be excluded as
outliers, some bias will remain from this effect. In particular, rescaled response
distance of random early responses to slow and medium dummy speeds (as they
have an exceptionally low angular speed) will be rescaled to very large response
distances. The effect of this error will be relatively small when analysing crab-
dummy distance, but can be observed in the analysis of rescaled crab-dummy
distance.

This error is independent of the actual position. Therefore I do not expect the
size of this error to change for responses close or far away from the dummy rail.

Delay As for the burrow entry response (see Section 5.1), we measure the onset of
the home-run response with a delay. This delay is expected to be shorter for
home-run responses than for burrow entry responses as we measure the onset
of movement rather than the crabs disappearing into the burrow.

If the crabs reacted to a speed-specific cue, the fastest dummies would be
furthest away at the time of reaction. If the visual cues were measured late, the
faster dummy will have approached the crab more than a slow one. This effect
would bias the observed decision criterion towards a distance-specific cue.

If the crabs reacted to a distance-specific cue, during this delay, the fast dummies
would approach even closer, causing the correlation between physical speed

and response distance to become negative (faster dummies would cause shorter response distance). This cannot be mistaken for another kind of visual cue.

The size of this error does not change with distance between crab and dummy rail for the home-run response (see Appendix B.1).

Neighbours Crabs may not only respond to their own perception, but to responses of their neighbours [Russo et al. 1998; Wong et al. 2005]. This would cause the affected responses to happen early as crabs only respond to their neighbour if they have not responded themselves yet. A crab responding to its neighbour effectively responds to the visual cues as seen by its neighbour, potentially with some delay.

The size of this error depends on the offset of the crab from the dummy rail. The closer the crab is to the dummy rail, the stronger the error introduced by a response to the neighbour.

This error depends on physical dummy speed and the position of the neighbour towards the crab with respect to the dummy rail. Neighbours that are in a direction directly away from the dummy rail will cause a larger error for faster dummies. Reacting to those neighbours could introduce a bias from a distance-based cue to an angular speed-based cue. Neighbours that are placed in the direction along the dummy rail will cause a larger error for slower speeds. This introduces a bias in the other direction. The bias introduced by a neighbour displaced along the dummy rail causes a larger bias. Assuming uniformly distributed neighbours, this would probably not cause any bias at all.

The size of this bias can be estimated as done in Appendix B.2. This effect is strongest close to the dummy rail. In addition, the probability that a crab is

affected by its neighbours decreases with increasing distance from the dummy rail.
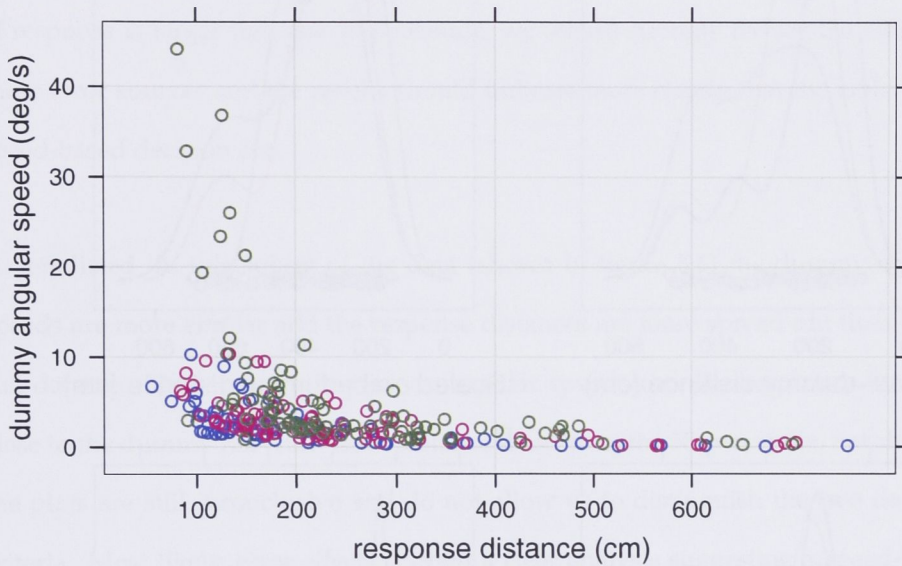
Figure 5.5: Home-Run Response Distance vs. Angular Dummy speed to determine outliers. Dummy angular speeds above $10°/s$ are excluded as outliers. So are responses at a distance of more than 500cm.

The influence of random responses can be reduced by removing outlier data points. Figure 5.5 shows response distance and dummy angular speed for home-run responses recorded in our experiment. Dummy angular speeds larger than $10°/s$ are treated as outliers. Also, reactions with a response distance larger than 550cm can be excluded as outlier data. This excludes very early responses to some external influence. However, not all early responses can be excluded in this way as random reactions to uncontrolled external influences for slow and medium speeds may have a smaller response distance than dummy-triggered reactions to fast dummies.
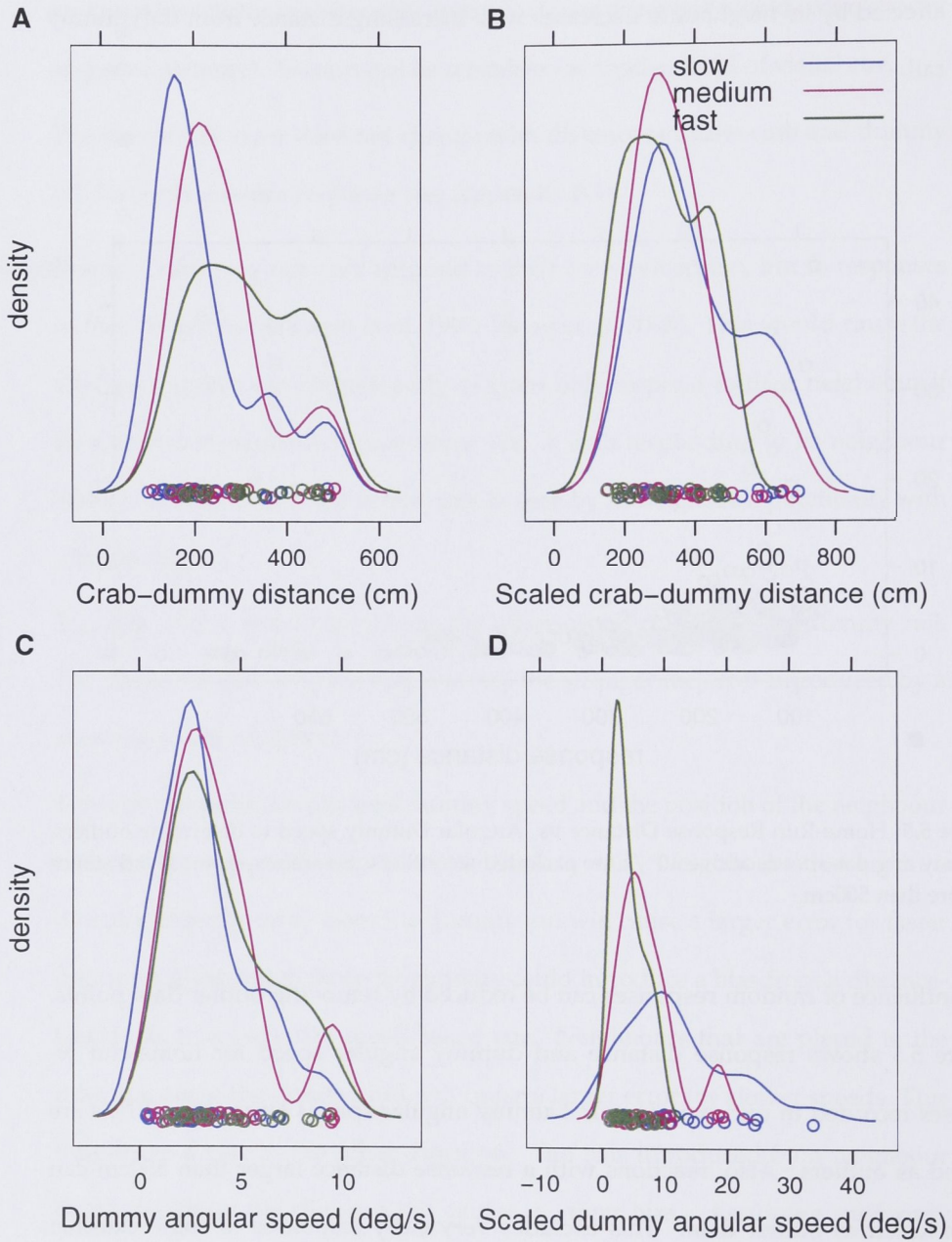
Figure 5.6: Visual Cues for Home-Run. (A) Crab-Dummy Distance, (B) Crab-Dummy distance that would have caused the observed angular speed had all dummies moved as fast as the fast dummy, (C) Dummy Angular Speed, (D) Dummy Angular Speed that would have been observed at the observed response distance had all dummies moved as fast as the fast dummy. These are the same plots as 5.4, but only responses that were in the upper half of crab-track distances were included.

The strongest disturbance effect, namely the early responses due to neighbours can be reduced by analysing home-run responses of crabs that are not directly approached by the dummy because they are positioned far away from the dummy rail. That means if we restricted our dataset to responses where the crab-track distance at time of response is larger than the 50-percentile, we would strongly reduce the effects of these error sources and the results should indicate more clearly that the crabs use a speed-based decision cue.

As predicted, in this subset of the data (shown in figure 5.6) the dummy angular speeds are more similar and the response distances are more spread out than in the full dataset. This strongly implies an angular speed cue. For responses by crabs close to the dummy rail (crab-track distance lower than the 50-percentile, not shown), the plots are still inconclusive and do not allow us to distinguish the two decision criteria. Most likely, error effects prevent a clear analysis suggesting a speed-based cue disturbed by errors also for these crab-track distances.

In addition to the analysis using plots, statistical models were fitted to the data of crabs not directly approached to determine the influence of physical dummy speed on crab-dummy distance and angular speed at the time of response. In these models, angular speed is correlated to physical speed, however at a low probability, whereas response distance is correlated much stronger (see table 5.1). Rescaled response distance is less dependent on physical dummy speed, however the influence is still significant. This is due to early responses at low speeds which, when rescaled, are beyond the cut-off limit for outliers. Rescaled dummy angular speed is, as predicted, strongly correlated to physical speed. These models suggest an angular speed-based cue.

Model	fixed effect	$F_{1,71}$	L.Ratio	p-value
angular speed	daspeed $\sim$ dspeed	3.920	3.895	0.0484*
scaled speed	scaled daspeed $\sim$ dspeed	31.736	28.002	$< .0001$
distance	cddist $\sim$ dspeed	19.866	18.343	$< .0001$
scaled distance	scaled cddist $\sim$ dspeed	4.711	4.631	0.0314

Table 5.1: Significance of influence of the dummy-speed as a covariate on respective visual cues for home-run. For F test, numerator df=1, denominator df=71, for likelihood ratio test df of model 5, df of null hypothesis 4 for all models. (N=114, 42 crabs in 15 setups). Data is for crabs in upper half of crab-track distances. - * not significant for F test

Reducing the dataset further to the upper 75-percentile of burrow-track distances makes these results even clearer, the number of observations is reduced strongly then. An improvement of significance is expected by the predictions of the error estimates (Model results not shown).

Spurious correlations and very high p-values could be caused by non-normality of the underlying distributions. A visual inspection of diagnostic plots of the final modes suggest that the model may be overestimating the significance of the reported effects.

For these reasons, a two-sided Kolmogorov-Smirnov test [Conover 1971, pp. 309-314] was also used to test whether the distributions of response distance and dummy angular speed for the respective dummy-speeds were equal. The results are shown in table 5.2. This non-parametric statistical test can verify whether two samples are drawn from the same continuous probability distribution.

If we look at results in columns 1 and 2 (slow vs. medium and slow vs. fast), the test confirms that the distributions of angular speeds are not significantly different ($p > 0.34$). Scaling the speed introduces large differences ($p < 0.0005$). Crab dummy distance distributions differ ($p < 0.002$), while the scaling, as predicted, removes this difference ($p > 0.15$).

Variable	slow vs. medium		slow vs. fast		medium vs. fast	
	D	p-value	D	p-value	D	p-value
angular speed	0.1081	0.9441	0.2146	0.3401	0.2273	0.2509
scaled angular speed	0.4398	< 0.0005	0.6052	< 0.0001	0.2727	0.103
cddist	0.4029	< 0.0019	0.5004	< 0.0002	0.2576	0.1412
scaled cddist	0.1069	0.9491	0.2588	0.1538	0.2879	< 0.0738

Table 5.2: Results for two-sided Kolmogorov-Smirnov test for pairwise comparison of distribution of variables at Home-Run. Only crabs with a larger burrow-track distance are included (larger than 50-percentile). ($N_{slow} = 37$, $N_{medium} = 44$, $N_{fast} = 33$)

The results in column 3 are not so clear, but overall the tests agree with the linear mixed model and support the hypothesis of an angular speed cue. Again, the results from column 3 are likely influenced strongly by outliers, because rescaling of response distances from responses to medium speed dummies created rescaled distances of more than 550cm, which the fast dummy could never reach, as those values were excluded as outliers.

The preceding two tests show that the crab's home-run decision is based on an angular speed cue. From this, we can make a prediction about the order in which crabs will respond. For the angular speeds observed (less than $10°/s$), crabs further away from the dummy rail will respond earlier. A measurement for the time of response relative to the dummy motion is the distance between crab and dummy projected onto the dummy track. I predict a positive correlation between crab-track distance and response distance along dummy rail. For higher physical dummy speeds the size of the effect is expected to be larger.

None of the three error sources discussed will create a false correlation. Moreover, as this test relies on response distances rather than speed to verify the visual cue for the response, the influence of the errors discussed in Appendix B will be small. Figure 5.7 shows a plot of distance from dummy rail vs. the distance along the rail at
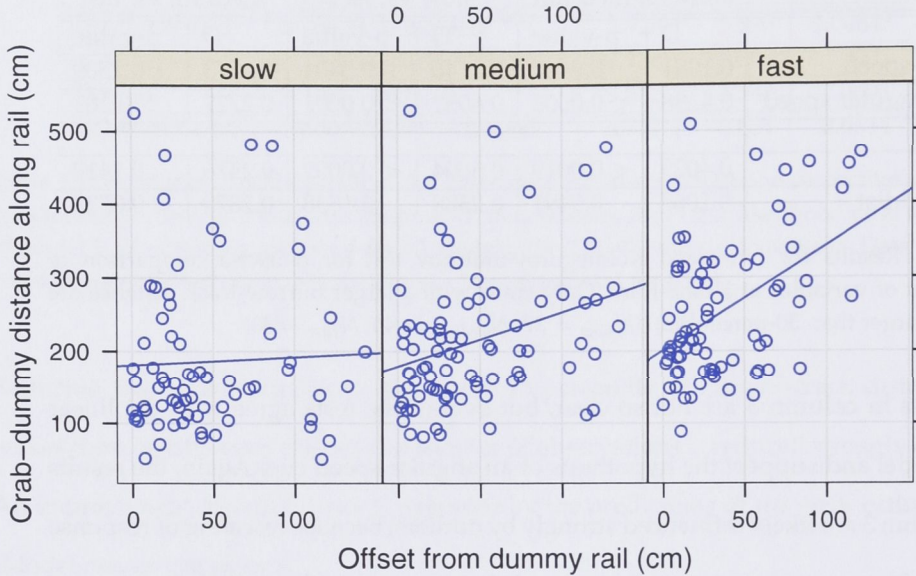
Figure 5.7: Response distance projected onto the dummy track over crab-track distance. The regression lines are fitted individually per plot.

Speed	Slope	Std
slow	0.1055	0.34778
medium	0.6910	0.39481
fast	1.4343	0.45167

Effect	numDF	denDF	F	p-value
speeds	2	164	9.8311	0.0001
hrctdist	1	164	8.5957	0.0039
speeds:hrctdist	2	164	5.0819	0.0072

Table 5.3: Coefficients and significance for influence of crab-track distance on crab-dummy distance along rail. Crab identity is used as random factor. P-values are calculated using Wald statistic approximation of F distribution (N=228, 59 crabs in 15 setups)

time of reaction for home-run responses. The regression lines have been fitted using regression per panel and not from the LME presented in 5.3, but corresponding slopes are similar. There is a positive correlation between crab-track distance and distance along dummy rail. This correlation is significant for medium and fast dummy speeds. It is larger for high dummy speeds. This follows the prediction.

5.4   The Burrow Entry Response

The burrow entry responses are analysed in a similar way to the home-run responses. The distributions of dummy angular speeds shown in figure 5.8C show three distinct distributions. In contrast, the crab-dummy distance at the time of the burrow entry in figure 5.8A are virtually identical. Rescaling dummy angular speed as described in A.1 removes the differences between observed dummy angular speeds - the peaks of the distributions shown in 5.8D are identical indicating that the effect sizes are as predicted by the experimental geometry. This data does not seem to suffer as strongly from the errors discussed for the home-run response. Burrow entry responses are less likely to be influenced by neighbour decisions as they happen late and each crab is already at its own burrow. In addition, I compensated for a delay of 400ms in measuring visual cues as described in section 5.1.

These plots suggest that burrow entry responses are based on a distance specific cue.

In order to apply a statistical test, we again have to remove outliers and responses with large leverage from the analysis. Figure 5.9 shows the burrow track distance and distance between the crab and the dummies projection to the ground for the recorded observations. The distance to the dummy over ground (2-D response distance) is used rather than the 3-D response distance, as this makes it very easy to mark the minimal response distance with respect to the burrow-track distance (red line). The dummy can never approach a crab closer than the burrow-track distance.

The mean response distance of all values is 60.5cm. This means, crabs entering their burrow which is further away from the dummy track than the mean response distance will always create a bias towards larger response distances as those crabs cannot
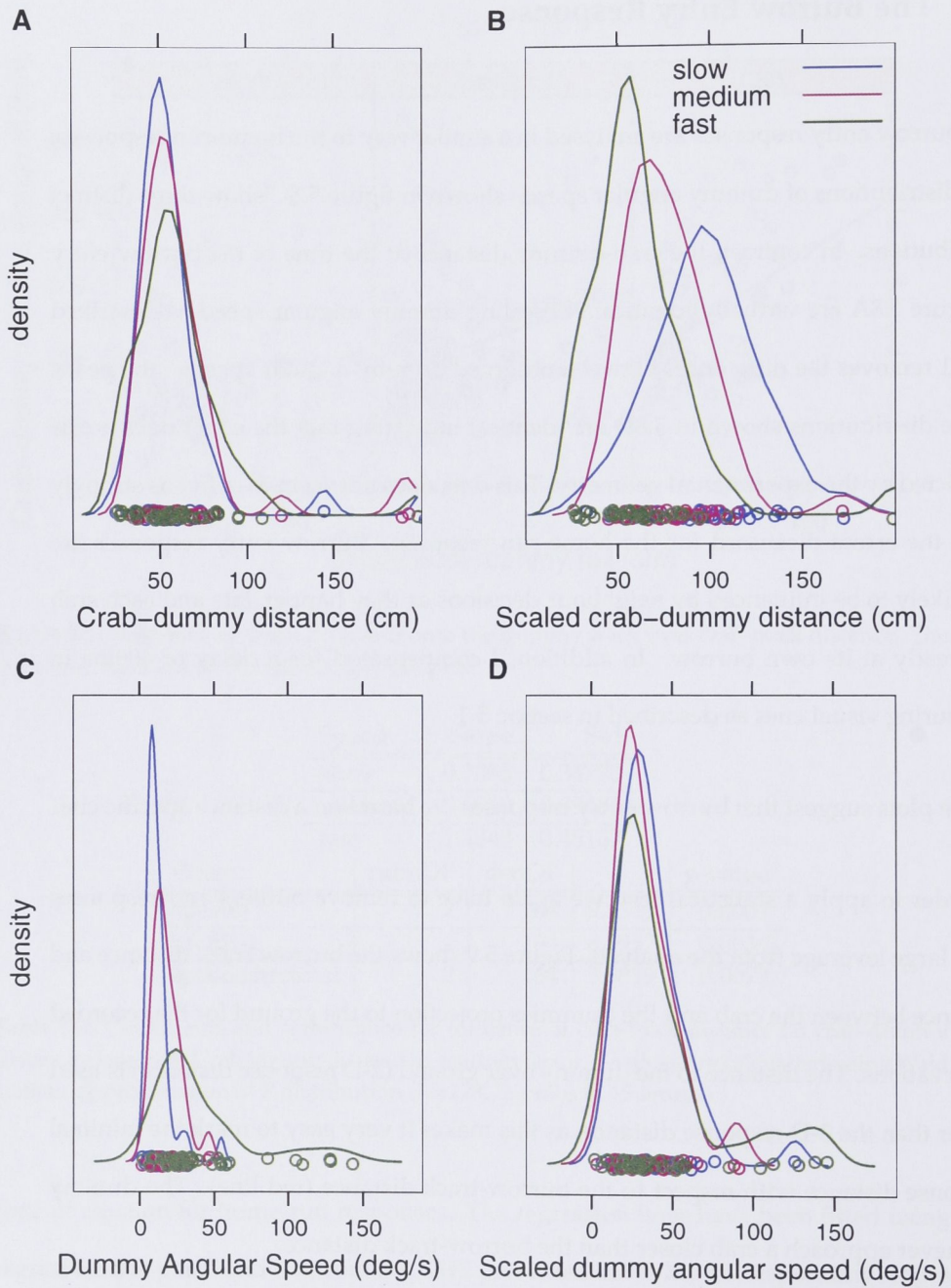
Figure 5.8: Visual Cues at Burrow Entry Decision. (A) Crab-Dummy Distance, (B) Crab-Dummy distance that would have caused the observed angular speed had all dummies moved as fast as the fast dummy, (C) Dummy Angular Speed, (D) Dummy Angular Speed that would have been observed at response distance had all dummies moved as fast as the fast dummy
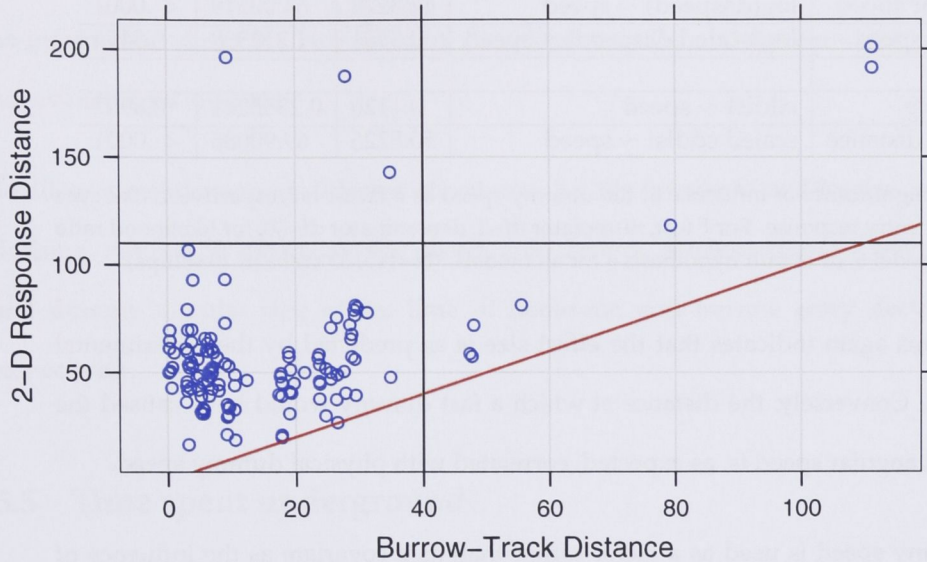
Figure 5.9: Response Distance (over ground) vs. Burrow-Track Distance for burrow entry response. Minimal response distance for a crab is larger than the burrow-track distance. Red line marks minimal possible response distance. Black lines mark criteria for outliers respectively.

respond below the mean response distance. Burrow entry reactions for burrows with burrow-track distances larger than 40cm are therefore excluded (to the right of the vertical black line). Also, three responses at a distance of more than 110cm over ground (above the horizontal black line) were also considered outliers and excluded.

An analysis using a linear mixed-effects model was performed. Results are shown in table 5.4. The model shows that the response distance is independent of dummy physical speed, while the dummy apparent speed at time of response is dependent on the physical speed. This influence of physical dummy speed on angular speed is simply due to the geometry. This is shown by analysing the rescaled dummy angular speed. The dummy angular speed a dummy would have caused at time of response if it had moved like a fast dummy (details see section A.1) is uncorrelated with physical

Model	fixed effect	$F_{2,80}$	L.Ratio	p-value
angular speed	log(daspeed) $\sim$ speed	44.3278	64.00519	$< .0001$
scaled speed	log(scaled daspeed) $\sim$ speed	0.5981	1.212538	0.5454
distance	cddist $\sim$ speed	0.1120	0.2315241	0.8907
scaled distance	scaled cddist $\sim$ speed	50.8226	69.90086	$< .0001$

Table 5.4: Significance of influence of the dummy-speed as a factor on respective visual cues for burrow entry response. For F test, numerator df=2, denominator df=80, for likelihood ratio test df of model 6, df of null hypothesis 4 for all models. (N=115, 33 crabs in 10 setups)

speed. This again indicates that the effect size is as predicted by the experimental geometry. Conversely, the distance at which a fast dummy would have caused the measured angular speed is, as expected, correlated with physical dummy speed.

The dummy speed is used as a factor rather than as a covariate as the influence of dummy speed is not necessarily linear at the given response distances. All models used camera identity and crab identity as random factors. Thereby influences from crab size, gender and relative burrow-track position on the response are attributed to the inter-crab variation. A visual inspection of the diagnostic plots showed that these models were acceptable.

From this model we could make a prediction about the time at which crabs enter their burrow. In contrast to the results from the home-run (figure 5.7), crabs that a closer to the dummy line are expected to react later. However, as the observed crab-track distances are small, the effect size is much too small to produce a significant result.

While it is quite clear that crabs use a distance-specific cue to decide when to enter the burrow, the specific visual cue used by the crabs in this experiment cannot be determined. As all experiments were done with dummies at the same height and same size, dummy elevation and dummy angular size are entirely determined by the dummy's distance from the crab. Though experiments with different sized

dummies and different dummy heights had been performed in earlier experiments, no information about the burrow entry stage was recorded and therefore data were not available for analysis.

To allow a comparison of different visual cues for the home-run and burrow entry decision, figure 5.10 shows angular speed, crab-dummy distance, dummy elevation and dummy angular size at the time of home-run and burrow entry decisions respectively.

5.5 Time spent underground

In this section I analyse the cues the crabs use to decide for how long they stay underground before reemerging. [Hugie 2003] predicted that prey waiting times would follow a positively skewed distribution. Also [Jennions et al. 2003] showed that crab waiting times are influenced by external cues. In their experiments, crabs hid longer if a looming-based stimulus was closer to the crab. Also they claim a marginally significant effect of approach direction on burrow waiting time using a different stimulus.

Both studies suggested that waiting times should be surprisingly short. [Jennions et al. 2003] found a mean waiting time of less than 50 seconds and 90% of the crabs had emerged within 2.3 minutes.

According to these studies, the distribution of waiting times should be positively skewed. Crabs should resurface quickly. Waiting times should be longer for small crab-dummy distances at time of burrow entry and slightly shorter for large crab-track distances.
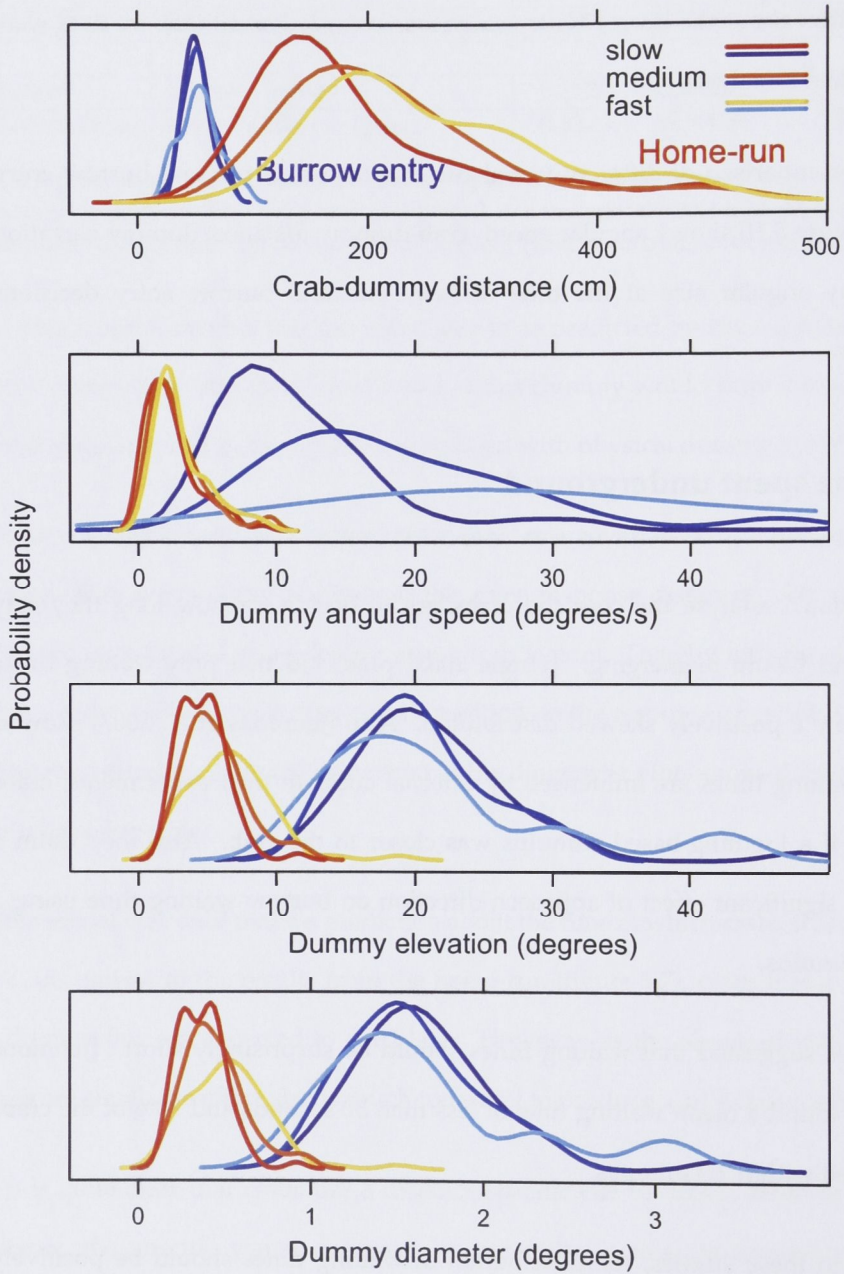
Figure 5.10: Plot of dummy angular speeds, crab-dummy distance, dummy elevation and dummy angular size for the home-run and burrow entry response
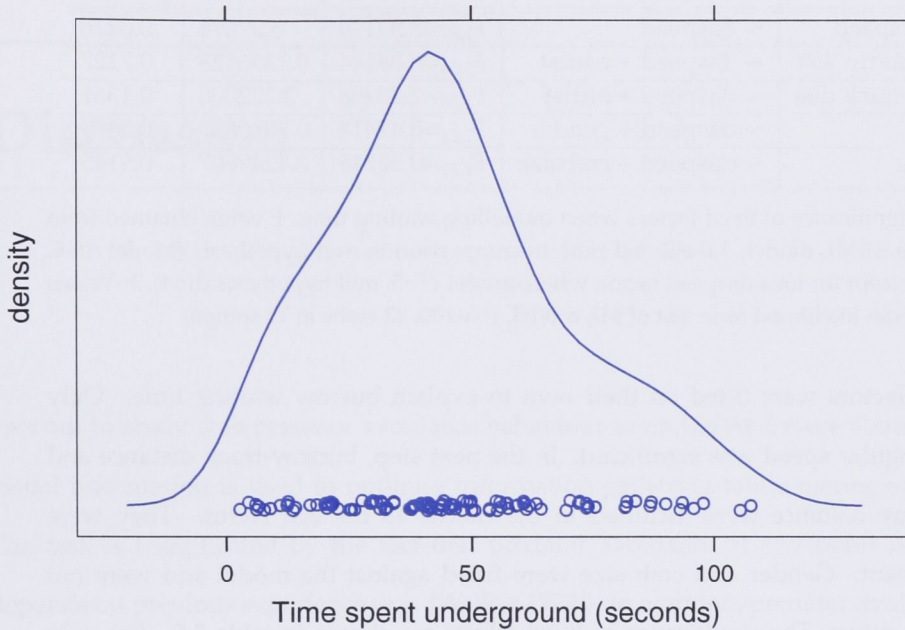
Figure 5.11: Density plot for waiting times after reaction to a dummy. Waiting times longer than 120 seconds excluded.

The distribution of waiting times to an approaching dummy is shown in figure 5.11. Waiting times that were longer than 120 seconds (approximately 10% of the data) were excluded from the plot. The distribution is clearly positively skewed. The median waiting time is 45.4 seconds, 90% of crabs had reemerged after 128 seconds.

I used mixed-effect models to estimate the influence of dummy angular speed at time of burrow entry, crab-dummy distance and the distance between the dummy track and the burrow. The distance between dummy track and burrow is the closest point the dummy reaches with respect to the burrow. The burrow-track distance is also a measure for the direction of approach. Burrows approached directly will have a small burrow-track distance.

Model	fixed effects	htb F	L-Ratio	p-value
angular speed	~ daspeed	$F_{1,67}$=5.37198	5.27874	0.0216
crab-dummy dist	~ daspeed + cddist	$F_{1,66}$=0.08144	0.1356128	0.7127
burrow-track dist	~ daspeed + btdist	$F_{1,66}$=2.26468	2.222000	0.1361
gender	~ daspeed + gender	$F_{1,21}$=0.41414	0.3610639	0.5479
crab size	~ daspeed + crabsize	$F_{1,21}$=0.36245	0.4249607	0.5145

Table 5.5: Significance of fixed factors when modelling waiting time. F value obtained from Wald test on REML model. Likelihood ratio in comparison to null hypothesis (Model df=6, Null df=5, except for lone daspeed factor, where model df=5, null hypothesis df=4). P-Values calculated from likelihood ratio test of ML model. (N=100, 32 crabs in 13 setups)

The three factors were fitted on their own to explain burrow waiting time. Only dummy angular speed was significant. In the next step, burrow-track distance and crab-dummy distance were included in the model as the last factor. They were not significant. Gender and crab size were fitted against the model and were not significant either. The significance of fixed-effects are shown in table 5.5. The only factor influencing burrow waiting time is dummy angular speed. Surprisingly, if the dummy's retinal image moved faster, crabs reemerged slightly earlier.

Discussion

I set out to study crab predator avoidance behaviour to understand more about how visual information is used to optimise information gathering while managing risk. The task is complicated by the fact that predator avoidance at any point in time depends on previous experience (e.g. [Walker 1972]). In addition, predator avoidance is organised into distinct stages, which depend on each other. This led to the idea to use a non-linear time series approach to identify temporal structures in the decision making process. The approach turned out to be inadequate for a number of reasons. Using a statistical analysis approach, I was able to show that while the home-run is triggered by a speed-specific cue, the burrow entry response is triggered by a distance-specific cue. The burrow waiting time before crabs reemerged was dependent on the angular speed observed by the crabs at an earlier point in time.

6.1 Analysis

Dealing with a sequence of behaviours needs a multi-stage approach. Firstly, the transitions between behavioural stages have to be identified. These transitions will be introduced as an outcome of a decision. After that, the extent to which later decisions are influenced by information gathered during previous stages of the behavioural

sequence need to be analysed. Knowing decision points and the interdependence of cues during different reaction stages, it is possible to investigate individual decisions by the means of a statistical analysis in order to identify relevant cues.

The initial hope was that the approach based on non-linear time series analysis would help me identify the decision points and the temporal interdependence during an escape response. The analysis would permit to determine this without any assumptions about the actual structure of the decision making process and without explicit formulation of temporal dependencies.

This approach failed. Decision models created by the clustering process could not be interpreted and they depended strongly on parameters of the clustering process. The dataset seems not to be suited for this kind of clustering. The algorithm was unable to deal with the high variability of measurements which were seemingly unrelated to actual decision making. The non-periodic structure and the short length of individual time series made clustering hard for an on-line algorithm. No good solution could be found to normalise traces such that similar behaviour sequences start and end in a similar state. This normalisation was needed, as otherwise the data would have been too sparse. However, this normalisation would have introduced exactly the assumptions the lack of which constitutes the core promise of this kind of non-linear time series analysis.

For data to be suited for such a kind of clustering, a system would need to be much less variable than the behavioural data with respect to the underlying dynamics. Even if the underlying dynamical structure is complicated (and potentially non-linear), it should be possible to capture the data in the network model, if the observations used for the clustering are unambiguously reflecting the underlying system dynamics.

[Webers and Zimmer 2005], for instance show how their clustering algorithm can successfully model a fractal attractor. However, for this experiment, the algorithm relied on a sample size (of several thousand samples) that is rarely available in biological datasets.

While it was not possible to extract decision points and relevant information from the data in an automated fashion, it is possible to pick information that is likely to be relevant by hand using insight into the behaviour. By reducing the analysis of decisions to the transition between response stages it was possible to apply a statistical analysis. To deal with the influence of decision history within an observation sequence, the dataset had to be restricted or previous observations had to be explicitly included in the analysis. Including previous information as covariates is difficult, however, as they are often correlated with each other. This causes stability problems in the statistical analysis.

For the analysis of the burrow entry response, all observations which did not show a home run response prior to the burrow entry response were excluded. For the analysis of re-emergence, in the decision of which crabs have to rely on information they have gathered prior to the burrow entry, this information was introduced explicitly by analysing the influence of the predation situation at burrow entry.

The employed statistical models have proven appropriate to analyse individual decisions. Dividing the response into the observed distinct stages in this way has proven useful for statistical analysis, and it may be interesting in future to incorporate this into new clustering algorithms. In order to describe the time-dependency of decisions, Markov-Chain models have an architecture that gives rise to modelling of memory while it is not necessary to specify time dependencies explicitly. They may

therefore prove useful to identify the temporal dependencies of behavioural decisions. Some initial ideas on how to model biological behaviour using Markov Chain models are given in [Metz et al. 1983].

6.2   Visual Cues

I was able to show that as predicted by [Hemmi and Zeil 2005], crabs employ different visual cues to make decisions at different stages during their escape behaviour sequence. This allows them to trade off risks imposed by predators against the costs of individual responses while improving the information content they gather.

6.2.1   Home-Run

Transferring results from the literature to this experiment, both distance-specific and speed-specific cues could have an influence on the home-run response. Two different visual cues triggering the home-run response are already known. [Nalbach 1990] showed in *Heloecius cordiformis* that a fixed increase in angular size is a visual cue triggering home-run. [Hemmi 2005b] showed that for *Uca vomeris* home-runs are triggered at very small angular sizes by a retinal speed cue. [Oliva et al. 2007] suggest that looming may be the relevant cue triggering a home-run response in their experiments on *Uca pugilator*, however they do not contradict [Hemmi 2005b], as during their experiments the angular size of the cue was larger than in [Hemmi 2005b]. It has been predicted that the particular geometry of predator size, speed and approach direction determine which cue would be triggered first [Hemmi 2005b]. When the visual image of a stimulus is expanding slowly (edge speed less than 0.5-1°/s) the increase in angular size seems to trigger an escape reaction. When presented

with movement faster than 1°/s of an individual edge or a stimulus, crabs seem to respond to angular speed. My experiment used faster dummies and my dummy was smaller than largest dummy in [Hemmi 2005b] and therefore it is even less likely that looming cues were relevant in my experiment.

The experiment presented here is very similar to [Hemmi 2005b]. [Hemmi 2005b] used dummy speeds of 19.5cm/s and 56.4cm/s, which are slightly slower than those used in this experiment (20.1, 36.2cm/s and 67.8cm/s, table 3.1). The angular speeds that elicited a response were smaller in this experiment (0.4-6.7°/s, figure 5.10) vs ($\sim 4°$/s) [Hemmi 2005b]. Jan Hemmi confirmed that the predation by birds was much stronger during this experiment than the one performed in [Hemmi 2005b]. This might have sensitised the crabs and reduced their response threshold.

The angular size at time of response in this experiment (0.4-1.4°, figure 5.10) is comparable to [Hemmi 2005b] (0.4-3°), but slightly smaller as would be expected due to a smaller dummy, higher physical speeds and higher sensitivity.

The small angular size speaks against a strong influence of a detection mechanism based on a looming cue as proposed by [Nalbach 1990]. Both experiments show that under these experimental circumstances, crabs base their decision when to run home on the angular speed of the dummy as perceived by the crabs.

Transferring the measured angular sizes and elevations to real birds, we can test the results for plausibility. Assuming a tern of size 30cm [Land 1999], the angular size of 1° corresponds to a bird that is 17m away from the crab. Based on the typical elevation of 5° at time of home-run response (figure 5.10), a tern flying at 2-3m height would be 23-34m away to have the same elevation. Both of these distances are rather large,

which suggests that the birds move relatively slower than the dummy used in this experiment.

The experiment presented here was able to show the relevance of an angular speed cue in the home-run decision for crabs that were far away from the dummy line. No conclusive result was found for crabs close to the dummy line. This is most likely due to interaction of crabs with their neighbours or responses that are triggered not by own observations but by a response to close neighbours [Russo et al. 1998; Wong et al. 2005] or a home-run response caused by an escaping crab approaching a crab's neighbour eliciting a burrow defence response as described in [Hemmi and Zeil 2003a]. Not only is the distortion effect stronger close to the dummy line, but the probability that there is a neighbour that is going to respond earlier is higher close to the dummy line. I determined the size of the influence of neighbours and the influence of reaction time on the results. The error induced by crabs responding to their neighbour's response is large enough to account for the observed errors. I therefore conclude that both the crabs away and the crabs close to the dummy rail respond using a speed-based cue to decide about a home-run. To exclude the influence of neighbours, crabs would need to be separated before confronted with a dummy predator eliciting a home-run response. Additionally, this would have to be done in the field, as [Nalbach 1990] found large differences in decision thresholds between laboratory and field experiments.

The error analysis pointed to a way on how to reduce the impact of neighbour interactions. When responding to an angular speed-based cue, crabs further away from the dummy rail would react earlier. Conversely this means crabs directly approached by the a predator respond later. This has been reported by [Hemmi 2005a], but he did not realize that this relation provides an easy and robust test for the

identification of the relevant visual cue. If crabs react later when approached directly, they react to an angular speed cue. If they react earlier, the cue is related to distance. Figure 5.7 shows the correlation between crab-track distance and the distance between the crab and the dummy along the rail at time of response - a measure for the earliness of a response. Crabs at larger offsets from the dummy rail indeed responded earlier when they were further away from the dummy line. This test relies on response distance only and therefore is less influenced by neighbour-interaction which have the largest impact on angular speed (see section B.2 for details).

6.2.2   Burrow Entry

For the burrow entry, the relevant visual cue or the set of relevant visual cues are distance-specific. Unfortunately, the setup of the experiment did not allow me to distinguish different candidates for distance-based visual cues. In this experiment, elevation, dummy angular size and looming (i.e. a fixed increase in angular size) all correlated perfectly. To distinguish these cues, new experiments need to be done with different dummy sizes, dummy heights and dummies which change in height during their approach.

Dummy angular size is a possible cue. The angular size at which the crabs retreated into their burrow was 2.9-6.3°, covering approximately 2-7 inter-ommatidial angles ([Zeil and Al-Mutairi 1996]). So crabs are able to measure angular size to some degree of accuracy. A tern of 30cm size at a distance of 2.7-5.7m would be seen with this angular size. In the first moment, this seems close. Assuming a tern is flying at 2-3m, this bird would be virtually over the crab when the crab responded to this angular size. However, responding this late is nevertheless still safe. To attack a crab, terns

need about 2-3 seconds between registering the crab directly underneath and touching the surface [Land 1999]. We have seen a delay of 400ms between the crab's decision to go underground and the time it has completely disappeared. This leaves an ample safety margin. This cutoff could be used to escape running birds as well. Plovers [Backwell et al. 1998; Hugie 2004] are a species of birds that run on the mud-flat in order to hunt for crabs. With a height of 20cm, they would cause a reaction due to angular size at a distance of 1.8-4.0m. This is far away though considering the relative safety, crabs are in at the entrance of their burrow.

The dummy in my experiment approached from far away, so the increase of angular size is equal to its angular size at response. According to [Nalbach 1990], a fixed size increase in the order of 11.8° elicited a response, which is three times the size recorded in my experiment. However, absolute thresholds are likely to vary significantly between species, populations, individuals and even time due to the context [Jennions et al. 2003; Reaney 2007]. Also, [Nalbach 1990] found large differences in response thresholds between lab and field experiments.

Elevation is another possible cue. Elevation was measured between 18-43°. A tern at 2-3m height with this elevation would be 2-9m away from the crab. This fits well with results obtained from the angular size. More importantly, this threshold is suited to protect against predators running on the ground. At 18°, a 20cm high bird [Hugie 2004] is at a 2-D distance of 61cm, at 43° elevation the bird would be at 21cm distance (over ground) from the crab. If the bird moves with 1m/s, a 400ms delay (allowing the predator to move by 40cm) between deciding to react and disappearing in the burrow would still almost be fast enough to escape this running predator.

Absolute angular size and elevation are coupled for predators on the ground. The highest point of a predator on the ground will correspond to its angular size in vertical direction. Also the increase in angular size is related to the final angular size (and thus elevation for ground-based objects) if an object approaches from far away.

6.2.3 Burrow Wait Time

If a crab wants to take into account information about the predator when deciding the time to resurface, it has to rely on previous information. No visual cues are available to a crab while it is in the burrow. In our experiment the waiting time was influenced by the the information crabs had when entering the burrow. I found that angular speed did have a significant influence on burrow waiting time, but the effect was small. If the dummy was fast at the time of burrow entry, crabs resurfaced earlier. This matches the marginally significant results from [Jennions et al. 2003], who found a significant influence for close looming cues but could not clearly show the influence of direction of approach on waiting time. My experiments also showed that burrow-track distance was marginally significant. Indeed, tangentially approached crabs will experience a higher angular speed. This could explain why a more direct approach will cause a longer underground time, even though high angular speed was shown to lead to a later home-run response ([Hemmi 2005b] and current results). This could mean that the function of a visual cue changes when animals have more information available. When angular speed is used as a home-run decision criterion, it is very loosely correlated to the actual real speed of the predator. When the crabs enter their burrow, however, they have more information about the predator's position and thus can estimate the physical speed of the predator.

My results do not agree with findings of [Jennions et al. 2003] that closer dummies elicited a longer waiting time. However their dummy in the distance experiment was a human standing up and sitting down quickly at 0.5m and 2.5m. Even though this would elicit higher angular speeds, the sheer size difference of these two stimuli is much larger than size differences experienced in my experiment. Any additional mechanism sensitive to angular size could explain the observed differences.

Re-surfacing faster after a fast predator passed through would also make sense if the predator is expected to continue moving without changing direction. A fast moving predator has flown past the burrow sooner than a slow moving predator. Another explanation for this effect could be that crabs seemed to learn when the dummy had passed their burrow as they sometimes surfaced almost immediately after the dummy passed their burrow (personal observation during video analysis).

[Hugie 2003] predicted the distribution of prey waiting times to be short and positively skewed when modelling the interaction between predator and prey as an evolutionary game. The predator waiting time distribution was also predicted depending on the prey waiting time. Predictions about predator waiting times and the relationship between predator and prey waiting times cannot be observed in an experiment with a dummy. Observation in real crab-predator interactions would be needed to verify Hugie's further predictions in this predator-prey interaction. [Hugie 2004] did this in *Uca princeps* and *Pluvialis squatarola*. The re-emergence time in my experiment is only about 60 seconds on average and thus fairly short, also, the distribution of waiting times is positively skewed. This matches Hugie's predictions. It is still surprising that predators would only have to wait for such a short time. This

is a perfect scenario for a sit-and-wait predator. And indeed the one tern observed at this location during several years of observations that employed a sit-and-wait strategy was highly successful (Hemmi, personal communication).

The fact that crabs employ different detection strategies for different stages in their response is not very surprising. Entering the burrow is a relatively expensive decision to make, therefore crabs should rely on a cue that accurately reflects actual predation risk. A distance-specific cue is better for this than a speed-specific cue, as the immediate danger from a predator is mainly dependent on the distance to the predator. The smaller the distance to the predator, the less time a crab has if the predator decides to attack. Even after a predator was identified, it is beneficial from an information perspective to observe the predator to gather more precise information about size, speed and approach angle. In this experiment, the real distance to the dummy was available through elevation and angular size, but even in real life, angular size is a good indication of the distance to an object if its size is approximately known.

The burrow waiting time should not dependent on the immediate risk imposed by the approach of a predator, but rather on the risk that the predator is still close to the burrow at time of re-emergence. It is not entirely clear why this risk should be determined by the angular speed. Studying bird hunting tactics [Ribeiro et al. 2004; Backwell et al. 1998; Land 1999] could be a way to understand this risk better. On the other hand, the effect size is small, so it could be an artifact of the particular experimental setup. One would expect that the direction of approach is significant but it was not in this experiment.

Analysing the re-emergence time exemplifies how information gathered by crabs during earlier response stages can be included in a statistical analysis for a specific decision. In this analysis this inclusion is simple, as it is easy to identify visual information potentially relevant to the decision. A crab can no longer get any information about the predator after it entered the burrow, hence it has to rely on the information it has gathered at the time of burrow entry. But the same principle can easily be applied to other decision stages if the temporal dependency is known.

Even though habituation plays a role for burrow entry decisions [Walker 1972], it was not included in this analysis. Also, further behavioural stages, such as the time spent at the burrow after resurfacing should be investigated in the future. However, this was not scope of this project.

The study of visual cues employed by crabs in their predator avoidance response and the fact that they organise their behaviour in stages shows how this species has adapted its perception anatomy [Land and Layne 1995; Zeil and Al-Mutairi 1996; Layne et al. 1997; Zeil and Hemmi 2006] and decision strategies to the environment they live in. Furthermore this environment can be used to simplify measuring distance not only between an object and oneself (as shown here for the burrow entry decision) but also between two points in the world (see [Hemmi and Zeil 2003b], which shows how fiddler crabs can determine distances between conspecifics and their burrow). These strategies are very likely useful for artificial mobile platforms as well, which often are used in a mostly two-dimensional world.

Reconstructing Perceived Dummy Speed

The (perceived) *dummy angular speed* depends on the (physical) *dummy speed* and the geometry, i.e. *crab-dummy distance* and the angle between *dummy velocity* and the *crab-dummy vector*. It can be calculated by projecting the *dummy velocity vector* onto the unit sphere around a crab.

Figure A.1 shows a visualisation of this calculation in two dimensions. The dummy position in the crab's retinal field is given by the intersection of the straight line connecting the dummy and the centre of the crab eye (we assume this is the crab position) and the unit circle around this position.

The velocity in polar coordinates, i.e. the rate of change of azimuth and elevation angles, is calculated by projecting the physical dummy velocity vector onto the line tangential to the unit circle at the projected dummy position using a central projection with the crab position as centre. This scales the length of the velocity vector depending on the crab-dummy distance.

For the three dimensional case, instead of a unit circle we will project the dummy position onto the unit sphere. After that, the physical dummy speed will be projected
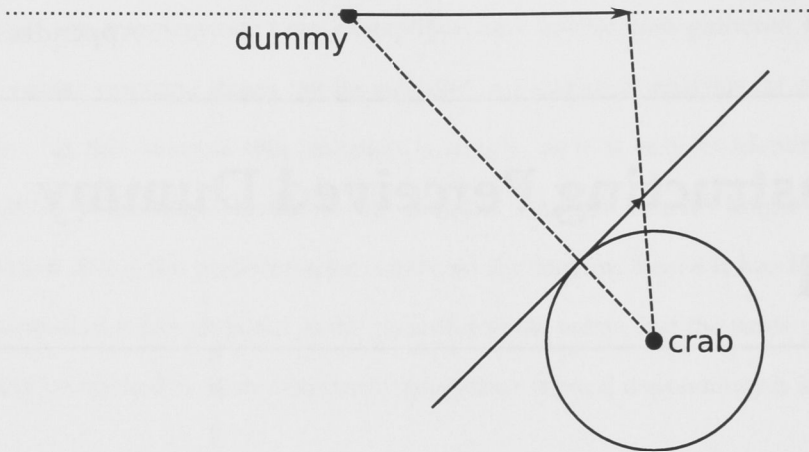
Figure A.1: Two-dimensional projection of dummy angular velocity calculation.

onto the plane tangential to the unit sphere at the projected dummy position. As the physical dummy position is above the horizon, the dummy angular velocity will have a non-zero elevation component, even though the physical dummy movement is parallel to the ground.

The dummy angular speed is given by the length of the dummy angular velocity vector. It is proportional to the physical dummy speed, the crab-dummy distance and depends on the angle between dummy physical velocity and the crab-dummy vector.

A.1　Scaling Perceived Dummy Speed

Given dummy speed v_d and perceived dummy angular speed ω, the scaled perceived dummy speed ω_{scaled} which would have been cause by a dummy with speed v_{scaled} is given by:

$$\omega_{scaled} = \omega \cdot \frac{v_{scaled}}{v}$$

A.2 Scaling Response Distance

Given dummy speed v and dummy angular speed ω for a certain geometry that gave rise to a response distance d, a scaled response distance d_{scaled}, at which a dummy with speed v_{scaled} would have caused an angular speed of ω can be calculated using the following procedure:

1. Rescale the time series $\omega(t)$ for all dummy positions during a dummy movement to v_{scaled} using A.1.

2. Find smallest time t_0 at which $\omega_{scaled}(t) \geq \omega$

3. $d_{scaled} = d(t_0)$

There are three points one has to take care of for rescaling response distance.

Crabs can move while the dummy is moving. Hence sampling dummy angular speed at a different point in time is not guaranteed to be based on the same geometry. This can be overcome by calculating $\omega_{scaled}(t)$ for the crab position at which the reaction happened.

It may not be possible to find a response distance when rescaling speed to a slower dummy, as the scaled angular speed may always be smaller than ω. Therefore, v_{scaled} should be chosen larger than v.

Finally, when rescaling an early response with small dummy angular speed to high speed, $\omega(t)$ could be larger than ω for all t. Calculating $\omega(t)$ for $t < 0$ may result in very large rescaled distances. Therefore in this case $d(0)$ is chosen as the rescaled crab-dummy distance.

Influence of Measurement Errors on Visual Cues

This appendix discusses error sources that mainly influence the home-run response. An estimate of the errors created by a delay in measuring visual stimuli is obtained and the influence of crabs responding to their neighbour's earlier response is demonstrated using several numerical examples. These examples are evaluated at typical response thresholds for the home-run response, where influence of neighbours is highest [Wong et al. 2005]. Where it is easily possible, the error analysis is extended to the burrow entry response.

This aim of this error analysis is to show how errors that were observed for response stages influence the ability to distinguish between angular-speed based cues and distance-based cues. Also we want to find out, how these errors change with the distance (offset) of the crab from the dummy line. It will show that a delay introduces a large error and bias in the response distance independent of the offset, while the influence on angular speed is small. Responses to neighbour's responses introduce a large error in angular speed, but less error in response distance. The error due to neighbours is reduced for larger offsets.
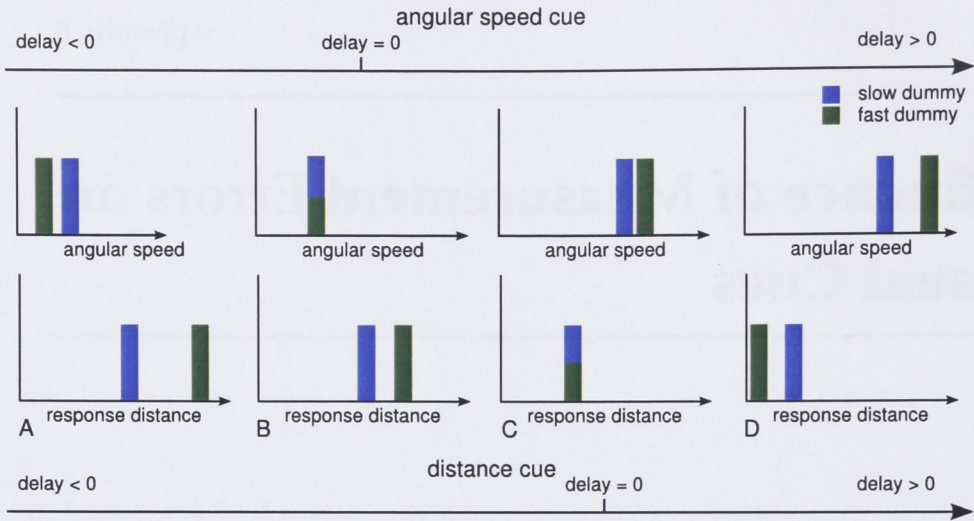
Figure B.1: Change of visual cues with respect to a delay in sampling.

B.1   Delay

There is a delay between the moment a crab made a decision and the moment it starts moving. Analysing the visual input at the time, the movement is first detected, will introduce a systematic bias in the data.

This analysis will proceed in four steps. In the first step a qualitative discussion analyses the direction of bias, while a second step will evaluate the size of the respective bias for the response distance. A third step will look at errors introduced by delayed sampling on angular speed. Finally, I will look at the effect of a delay on the burrow entry response. The quantitative analysis will look at sample delays of multiples of 200ms, as this is the frame interval encountered in the real data.

B.1.1 Qualitative Bias

Figure B.1 gives an overview over the relationship between dummy angular speeds and response distance measured with different delays around the actual decision point. The rectangles represent one particular representative measurement. If the decision was made using an angular speed cue, angular speed and response distance should look like figure B.1B. If visual input is sampled too early, it will look like figure B.1A. If the visual input is sampled too late, it will look like a distance-specific cue (figure B.1C). If the decision was made based on a distance-specific cue, the measurements will look like B.1C. If the visual information is sampled too early it will look like B.1B and could be wrongly interpreted as an angular speed cue.

B.1.2 Effect of Delay on Response Distance

To quantify the size of the delay effect, I will first calculate correct response distances for an angular speed-based cue. Then I will analyse how these response distances change with respect to a sampling delay depending on different crab-track distances (offsets).

Figure B.2 shows the crab-dummy distance over time. The curves are virtually linear for crab-dummy distances larger than 1.5 times the offset. The angular speed threshold is exceeded well before that.

For my experiment, I assume a response threshold of $2°/s$, and dummy speeds of a slow dummy at 20cm/s and a fast dummy at 80cm/s. I consider three crabs at an offset of 0cm, 60cm and 120cm from the dummy rail. Their correct response distances would be:
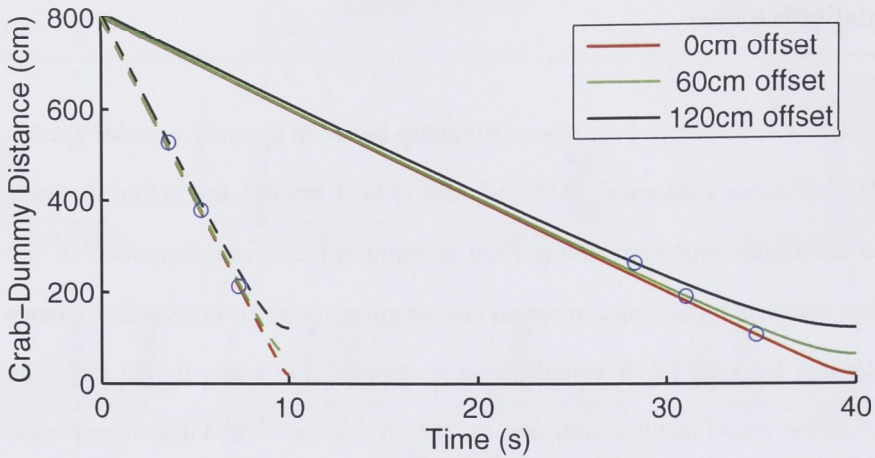
Figure B.2: Crab-Dummy Distance over time for different dummy speeds (20cm/s and 80cm/s) and offsets. The blue circles mark the time of reaction for a $2°/s$ angular speed threshold.

offset	distance slow dummy	distance fast dummy	spread
0 cm	106 cm	209 cm	103 cm
60 cm	189 cm	373 cm	186 cm
120 cm	264 cm	526 cm	262 cm

The spread is the difference in response distance for the two speeds. If through a delayed measurement this spread is reduced to 0cm or a value much less than half the expected spread, the observation could be mistaken for a decision based on distance rather than angular speed.

As crab-dummy distance is linear with respect to time at the typical response distance for home-run responses, a change in delay will cause a fixed error in response distance independent of the offset. This error only depends on the physical dummy speed. The spread will therefore change with the difference of physical dummy speeds, i.e. 60cm per second of delay. If we for instance measured 200ms (one frame) late, the spread would be reduced by 12cm.
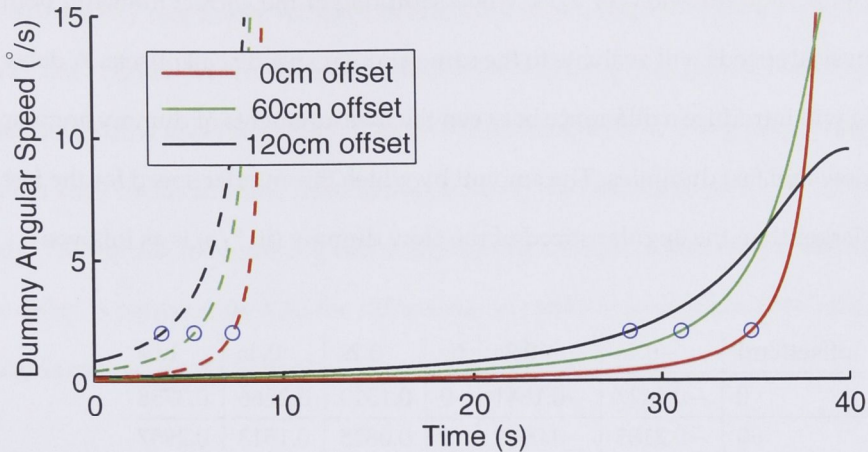
Figure B.3: Dummy angular speed over time for crabs at different offsets and different physical dummy speeds (20cm/s and 80cm/s). Blue Circles represent times, where reaction occurred for respective speeds.

In case of the home-run, with respect to response distance, a sampling delay of less than one second will not destroy the spread allowing us to distinguish an angular speed cue versus a distance-based cue. The spread will be larger for larger crab-track distances (offsets), making the response distance even more robust against a delay.

B.1.3   Effect of Delay on Angular Speed

Figure B.3 shows a plot of dummy angular speed over time. The blue circles mark the point in time at which a reaction threshold of $2°/s$ was exceeded. A time delay in sampling will increase dummy angular speeds more for fast dummy speeds (dashed lines) than for slow dummy speeds (solid lines). The rate of change is smaller for larger offsets. This is independent of the actual threshold.

At an offset of 120cm, the slow dummy reaches a maximum angular speed of $8°/s$. So angular speed thresholds above this level cannot be used reasonably for comparisons.

Assuming a decision threshold of $2°/s$, when sampling at the correct moment, both dummy physical speeds will evaluate to the same angular speed at all offsets. A delay in sampling will introduce a difference between the measurements of dummy angular speed for slow and fast dummies. The amount by which the angular speed for the fast dummy is larger than the angular speed of the slow dummy (in $°/s$) is as follows:

offset(cm)	−0.4s	−0.2s	0s	0.2s	0.4s	1.0s
0	−0.4427	−0.1841	0	0.1319	0.2266	0.3758
60	−0.2185	−0.0992	0	0.0825	0.1513	0.2957
120	−0.1487	−0.0696	0	0.0612	0.1149	0.2402

For reaction thresholds common in the home-run response, delays introduce a spread in measurements of angular speed of less than $0.5°/s$ for a delay of $−0.4$-1s. The changes are smaller for crabs with large crab-track distance.

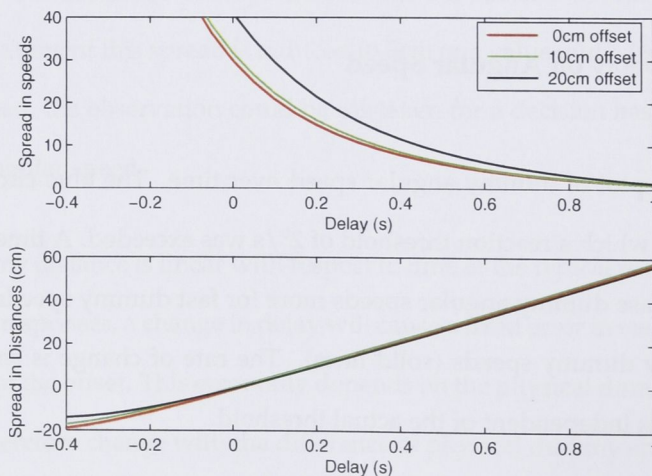## B.1.4 Delay in burrow entry responses

Figure B.4: Change of visual cues with delay for burrow entry decision, assuming a distance threshold of 50cm

For burrow entry responses, we have to analyse a shift of angular speeds relative to a distance cue. Figure B.4 shows these values with respect to a delay. As the offsets are smaller for burrow entry decisions, effects of this offset are low. The peaks of response distances shift linear in time, introducing shifts in the distributions for small offsets already. The spread in angular speed shifts rapidly for delays less than 0, but as long as the delay is between 0s-0.4s, the differences in peaks of more than $8°/s$ will make the angular speed peaks look like a distance-based cue.

B.1.5 Summary

Measurements of dummy angular speed and crab-dummy distance at the time crabs start moving for a home-run resemble the situation depicted in figure B.1B, but are shifted slightly towards figure B.1C. The crab has made its decision when it started moving, so the delay between the decision and our measurement is positive but small. The bias due to the delay measurement will be towards a distance-based cue.

At the time the crabs disappear in their burrow, measured angular speed and crab-dummy distance look like B.1D. We are sure to have a considerable positive delay. From external consideration made in section 5.1, we can estimate a delay of 400ms.

To allow analysis of the measured data, we compensate the delay. If the applied compensation is correct within -200 to 800ms, the dummy angular speeds allow the detection of a distance-specific cue, as the peaks of the angular speed distribution will still differ. Response distance is much more sensitive to the delay.
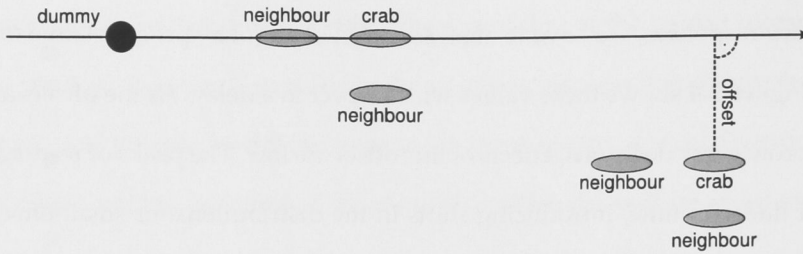
Figure B.5: Schematic plot of two crabs with offset 0 and larger offset, and potential neighbouring crabs that would respond earlier.

B.2 Neighbours

Crabs are known to react not only to their own perception but also to fleeing neighbours [Russo et al. 1998; Wong et al. 2005]. Freeze and home-run responses are commonly excited by neighbours, whereas influence of neighbours on burrow entry decisions is low. That's why this error discussion focuses on the home-run decision.

A crab responding to a neighbour's response acts as if it effectively responded at a different position. Its reaction will occur earlier - otherwise it would have reacted to the visual cue visible at its own position. As seen in figure B.3, crabs with larger offsets experience larger angular speeds. Neighbours along the direction of the dummy rail towards the approach direction of the dummy or perpendicular to the dummy having a larger offset will therefore react earlier to an angular speed cue. Two crabs and their potential neighbours are depicted in figure B.5.

I will sample both cases: The error introduced by a neighbour that is 30cm further away from the dummy rail and the error introduced by a neighbour that is 30cm towards the approaching dummy.
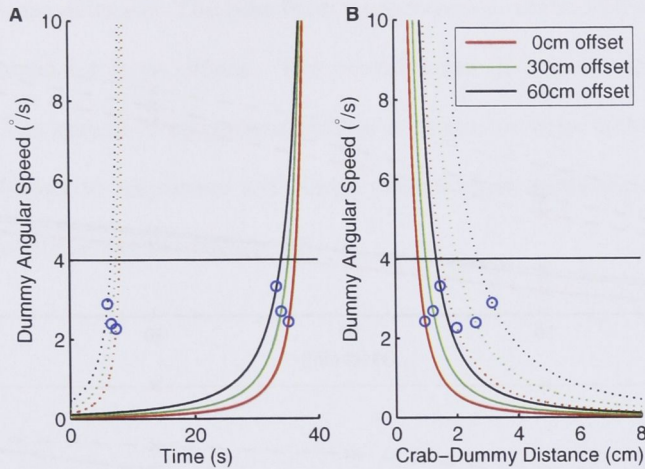
Figure B.6: Crab-dummy distance and dummy angular speed plots. Blue circles mark the measured visual stimuli, if the crab responded to neighbour. The black line marks the actual response threshold (4°/s).

Figure B.6A shows for an example threshold (2°/s) how the angular speed is reduced at the time of reaction due to a reaction to a neighbouring crab. In figure B.6B, one can read of the influence of the response to a neighbour to the response distance. The black line in both plots marks the actual decision threshold.

If the neighbouring crab is not placed perpendicular towards the dummy rail, but ahead directly in the direction of the dummy, reacting to this neighbour would increase the crab-dummy distance by a fixed offset. A slow dummy needs 1.5 seconds to cover 30cm distance, a fast dummy needs 0.375s. This would introduce a constant offset in the response distance. The reduction in angular speed can be observed in figure B.7.

Figure B.7 shows the correct response distance (B.7A) and angular speed (B.7B) at the time of response and when the decision was caused as a reaction to a neighbour for different offsets. Actually, for an offset of 120cm, the neighbour perpendicular away
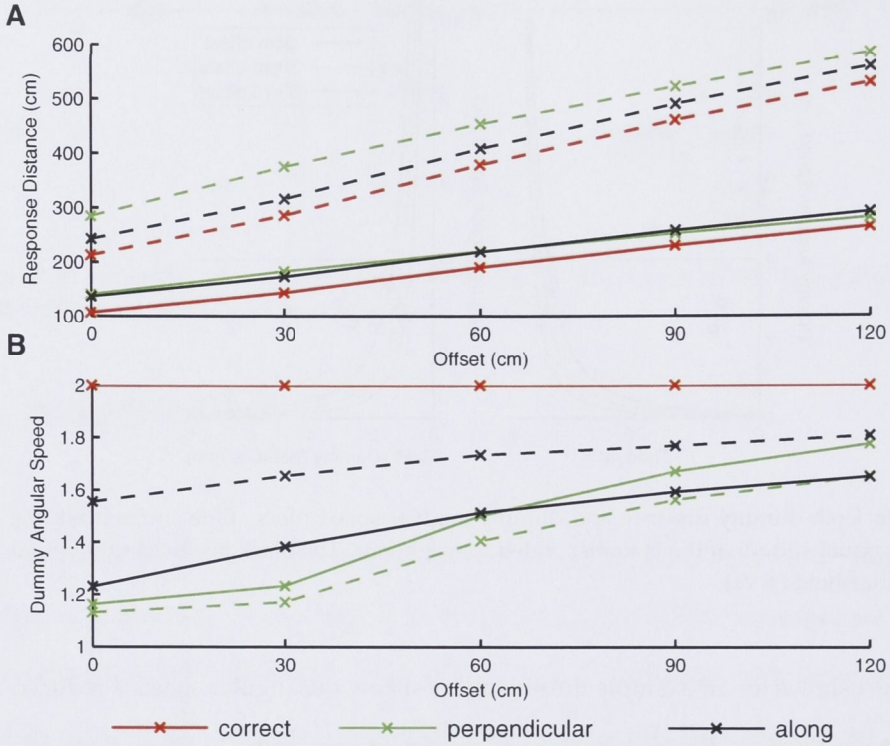
Figure B.7: Response distance (A) and dummy angular speed (B) for response by crab (red), response to a neighbour crab away from the dummy line in a perpendicular direction (green) and response to a neighbour ahead along the dummy line (black) shown for a dummy speed of 20cm/s (solid line) and 80cm/s (dashed line). Response criterion: angular speed threshold $2°/s$

from the dummy track would have reacted later than the crab. While the reaction to neighbours reduce the angular speed substantially (up to 40% for a 0cm offset) and the bias in angular speed changes depending where the neighbour is, the resulting errors in response distance are small. The spread between response distances is maintained. Reactions to neighbours will most strongly affect the angular speed, but less so the response distance. The size of the error due to neighbours reduces for large offsets.

Summarising, the home-run response will most strongly be affected by neighbours. Responses to neighbours have a very strong effect on dummy angular speed, but

less so on response distance. The bias from perpendicular crabs and crabs along the dummy line cancel for large offsets. The overall error in angular speed is less for larger offsets. The spread in response distance is larger for large offsets, that is why reducing the dataset to responses with large offsets when analysing angular speed improves the results as seen in section 5.3.

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