

Heterospecific timing of waving display in ocypodid crabs *Ilyoplax pusilla* and *Uca lactea*

Naohiro Aizawa

Graduate School of Human and Environmental Studies, Kyoto University, Kyoto 606-8501, Japan.

E-mail: n_aizawa@gaia.h.kyoto-u.ac.jp

This study explores whether timing adjustment in ocypodid waving also occurs between heterospecific pairs. Analysis of the dyadic interactions between neighbouring males of *Ilyoplax pusilla* and *Uca lactea* in the field showed that the former tended to wave with some delay after each *U. lactea* wave, while the latter was little influenced by *I. pusilla* waves. The heterospecific wave timing of *I. pusilla* by *U. lactea* waves can be viewed as a weakened form of the conspecific wave timing mechanism in this species.

Male ocypodid crabs commonly engage in waving displays, characterized by a species-specific movement pattern of the chelipeds. Recent studies (Backwell et al., 1998; Aizawa, 1998) have shown that in two species of ocypodids, neighbouring conspecific wavers mutually adjust their wave timing, resulting in synchronous waving of neighbours. Signal timing can be perturbed by signals not only of conspecifics, but also of heterospecifics with similar displays (Schwartz & Wells, 1983). This paper describes how two sympatric species of ocypodids, *Ilyoplax pusilla* de Haan and *Uca lactea* de Haan (*U. lactea lactea*), time their waving according to a heterospecific waver nearby. The males of *I. pusilla*, the most active waver among Japanese ocypodids, exhibit rhythmic waves repeated in ~1 s cycle, and neighbouring individuals show a strong tendency to start each wave simultaneously (Aizawa, 1998). The waving of an *U. lactea* male, although active, has longer and more variable wave periods. The two species differ greatly in size and motion patterns of waving. Each *I. pusilla* wave consists of a rapid vertical stroke of both chelipeds, which have no apparent asymmetry (Aizawa, 1998). A wave of *U. lactea* is a complex sequence of strokes of the major claw (Crane, 1975). It typically consists of more than one up and down movement of the major claw.

The research was conducted on an intertidal sandy mudflat in the Chikusa River Estuary, Hyogo Prefecture, Japan. Waving displays of ten pairs of *I. pusilla* and *U. lactea* males, whose burrows were spaced about 10–15 cm apart, were video recorded in June and July, when the waving of both species is most active. Since both species live at high density, such short distances between the burrows are common in this area. The pairs were visually isolated from other neighbouring *I. pusilla* males by inserting opaque boards between them, to prevent the influence of their vigorous waving. The videotapes were analysed frame by frame, the onset time of each wave was noted, and intersignal intervals and delays were calculated. Intersignal intervals of an individual in a pair are time intervals between the onsets of successive waves of that individual. A delay of an individual in a pair refers to the time interval between the onset of a wave of that individual and the preceding wave of another in the pair (see Figure 1). Calculating the delays for the entire data yielded a distribution of the delays for each individual in each pair. The further analysis was whether a test statistic of each distribution deviated from that of the null distribution wherein two individuals do not influence the other's wave timing. For that purpose, a program for a randomization test was written, which creates randomized, null distributions by reshuffling and sampling of the original data (Minckley et al., 1995).

Figure 1A & B shows the pooled distributions of the delays for ten individuals of *I. pusilla* and *U. lactea*, respectively. The former distribution had a valley over small delay values, while the latter lacked such tendency. The results of the randomization test are given in Figure 2. Each line in the figures represents the result for one individual. Six points on each line indicate that the proportions of the delays (d) within $0 < d = 0.3$ s, $0.3 < d = 0.6$ s, $0.6 < d = 0.9$ s, $0.9 < d = 1.2$ s, $1.2 < d = 1.5$ s and $1.5 < d = 1.8$ s (from left to right) in the distribution of the delays for each randomized data set were equal or less (Figure 2A & C)/equal or more (Figure 2B & D) than those of the original data of the corresponding individuals in ND times of the total 10,000 runs. If ND is less than 250 in Figure 2A & C, or Figure 2B & D, this means that the value of the test statistic (the proportion of the delays within the corresponding range) in the original data is included in the lower or upper, respectively, 2.5% extreme of the distribution of the test statistics obtained from the randomized data, which corresponds to the satisfaction of a 5% significant level in a two-tailed statistical test.

The results for *I. pusilla* are shown in Figure 2A, B. In Figure 2A, seven, six and two of ten individuals scored the values of ND lower than 250 for the ranges of $0 < d = 0.3$ s, $0.3 < d = 0.6$ s and $0.6 < d = 0.9$ s, respectively. In Figure 2B, four, four and two of ten individuals scored the ND values less than 250 for the ranges of $0.9 < d = 1.2$ s, $1.2 < d = 1.5$ s and $1.5 < d = 1.8$ s, respectively. In Figure 2C, D, which shows the results for *U. lactea*, only three and four points, respectively, scored the ND values less than 250, each of which points were distributed in the ranges of $0 < d = 0.3$ s, $0.6 < d = 0.9$ s and $1.2 < d = 1.5$ s in Figure 2C, $0 < d = 0.3$ s, $0.3 < d = 0.6$ s, $0.6 < d = 0.9$ s and $1.2 < d = 1.5$ s in Figure 2D. The randomization test thus revealed that, in *I. pusilla*, the occurrence of the waves tended to be less frequent than expected by chance until about 0.9 s after each *U. lactea* wave, and tended to be concentrated for $d > 0.9$ s. In *U. lactea*, the infrequent occurrences of the points with ND values less than 250 and their inconsistent distribution suggest little influence of *I. pusilla* waves.

The conspecific synchronous waving in *I. pusilla* is a consequence of each individual having a specific timing mechanism called phase delay synchrony (Aizawa, 1998). In phase delay synchrony, an individual starts its own signal after a constant delay from each signal of a neighbour, and the delay is close to its free running (spontaneous) signal period. However, the neighbour's signal delivered immediately before the onset of one's signal can not affect the timing of that signal any more, since the signal has been already triggered (Buck et al., 1981; Greenfield, 1994). Under this algorithm, the distribution of the

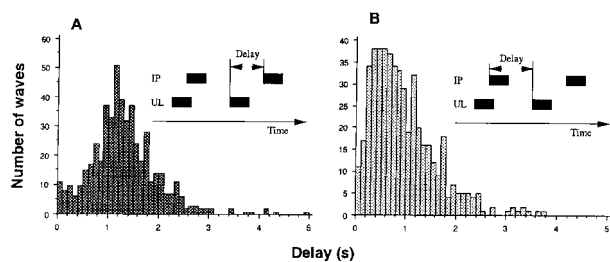


Figure 1. Pooled distributions of the wave delays for ten individuals of (A) *Ilyoplax pusilla* (N of each ind=15–139) and (B) *Uca lactea* (N of each ind=15–142). Schematic representation of delay is also shown inside each graph (Each rectangle indicates one wave. IP, *I. pusilla*; UL, *U. lactea*).

wave delays has two distinct groups, separated by a gap within which the waves rarely occur (Aizawa, 1998). One group is composed of the waves started immediately after the onset of the waves of a neighbour and corresponds to the waves that have been already triggered before the preceding waves of a neighbour, and the other is of the waves started after the delay approximately equal to the free running wave period.

The distribution of the delay of *I. pusilla* waves to *U. lactea* waves was basically similar to that of the conspecific interactions of *I. pusilla*. A delay of shorter than ~1 s, which approximates the modal free running wave period of *I. pusilla*, was infrequent in both distributions (Aizawa, 1998). Although the former distribution lacked a clear peak near 0 s delay, this might be due to the up and down motion of the minor claw and the walking legs of *U. lactea*, motion which often precedes slightly the onset of the major claw movement in *U. lactea* waves. This motion, although too inconspicuous in the video images to use them as an index of the onset time of the waves, possibly affects the timing mechanism of *I. pusilla* slightly before the onset of the major claw movement. These suggest that the heterospecific and conspecific wave timing share the same proximate basis, despite the great difference in motion patterns of waving and size between *I. pusilla* and *U. lactea*. Compared to the conspecific interactions, the effect of *U. lactea* waves seems to be relatively weak, as shown in the high occurrences of *I. pusilla* waves with a delay of 0.3–0.9 s after *U. lactea* waves. The heterospecific timing of *I. pusilla* waves by *U. lactea* waves thus can be viewed as a weakened form of the conspecific timing mechanism. But even if so, this does not necessarily mean that the heterospecific wave timing has no selective advantage.

Recently, Backwell et al. (1998) found that the fiddler crab *Uca annulipes* exhibits synchronous waving among neighbouring males, and that the males visited by females tend to wave slightly before its neighbours. These studies indicate the possibility of preference for leading waves in *I. pusilla*.

One hypothesis on the cause of the preference for leading acoustic signals is that it is derived from the basic property of the acoustic system such as the masking effect of leading acoustic stimuli (Greenfield, 1994). Support for this notion is that the phenomenon wherein an animal fails to respond to the second of two temporally close acoustic stimuli is known in various animals, in contexts other than mate choice (Greenfield, 1994). Under this hypothesis, the female preference can be affected by salient acoustic stimuli other than conspecific signals. If *I. pusilla* also possess the preference for leading waves, and it is based on the general property of the visual system originally selected in contexts other than mate choice, it may be advantageous for *I. pusilla* males to delay their waves in response to heterospecific waves as well as conspecific ones.

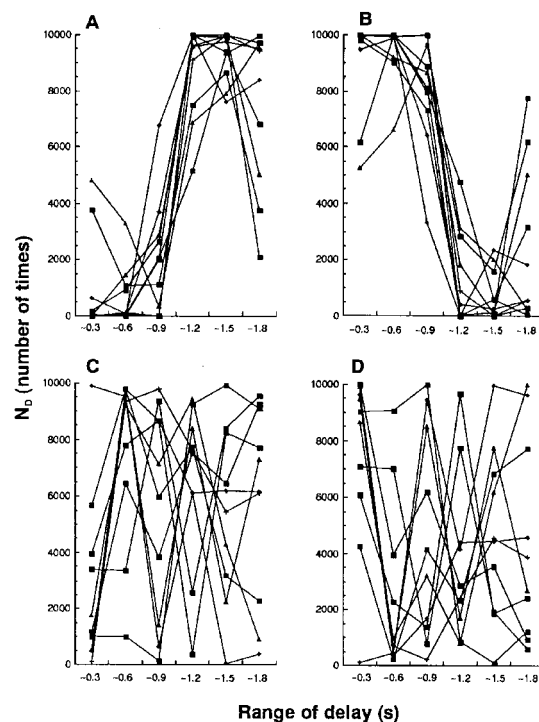


Figure 2. Results of the randomization tests for (A, B) *Ilyoplax pusilla* and (C, D) *Uca lactea*. The test created 10,000 randomized distributions of the wave delays by reshuffling and sampling of the original data, and compared each time the test statistic (the proportion of the delays within a certain specified range) of the original data and the randomized data. Each line in the figures represents the result for each individual. Six points on each line indicate that the proportions of the delays (d) within $0 < d = 0.3$ s, $0.3 < d = 0.6$ s, $0.6 < d = 0.9$ s, $0.9 < d = 1.2$ s, $1.2 < d = 1.5$ s and $1.5 < d = 1.8$ s (from left to right) in the distribution of the delays for each randomized data set were equal or less (A, C)/equal or more (B, D) than those of the original data in ND times of the total 10,000 runs. A point with a ND value less than 250 indicates that the proportion of the delays within the corresponding range was smaller (A, C)/larger (B, D) than expected by a chance at a 5% significant level.

I thank M. Kato for comments on the manuscript.

REFERENCES

- Aizawa, N., 1998. Synchronous waving in an ocyropid crab, *Ilyoplax pusilla*: analyses of response patterns to video and real crabs. *Marine Biology*, **131**, 523–532.
- Backwell, P.R.Y., Jennions, M.D., Passmore, N.I. & Christy, J.H., 1998. Synchronized courtship in fiddler crabs. *Nature, London*, **391**, 31–32.
- Buck, J., Buck, E., Case, J.F. & Hanson, F.E., 1981. Control of flashing in fireflies. V. Pacemaker synchronization in *Pteroptyx cribellata*. *Journal of Comparative Physiology*, **144A**, 287–298.
- Crane, J., 1975. *Fiddler crabs of the world*. New Jersey: Princeton University Press.
- Greenfield, M.D., 1994. Cooperation and conflict in the evolution of signal interactions. *Annual Review of Ecology and Systematics*, **25**, 97–126.
- Minckley, R.L., Greenfield, M.D. & Tourtellot, M.K., 1995. Chorus structure in tarbush grasshoppers: inhibition, selective phonoreponse and signal competition. *Animal Behaviour*, **50**, 579–594.
- Schwartz, J.J. & Wells, K.D., 1983. An experimental study of acoustic interference between two species of neotropical treefrogs. *Animal Behaviour*, **31**, 181–190.

21 June 1999. Accepted 7 September 1999.