

surprise that a low-level sensorimotor manipulation systematically influences the behavior in a task only implicitly evoking the notion of number magnitude. However, sensory and motor processes, which have originally evolved for basic interactions with the environment, are reportedly exploited during abstract cognition [15]. Intriguingly, as head turning can influence one's spontaneous spatial exploration, it also appears to affect predictably the apparent spontaneity of 'random' numerical choices.

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References

1. Hubbard, E.M., Piazza, M., Pinel, P., and Dehaene, S. (2005). Interactions between number and space in parietal cortex. *Nat. Rev. Neurosci.* 6, 435–448.
2. Fischer, M.H., Castel, A.D., Dodd, M.D., and Pratt, J. (2003). Perceiving numbers causes spatial shifts of attention. *Nat. Neurosci.* 6, 555–556.
3. Loetscher, T., and Brugger, P. (2007). Exploring number space by random digit generation. *Exp. Brain Res.* 180, 655–665.
4. Gottlieb, J. (2007). From thought to action: The parietal cortex as a bridge between perception, action, and cognition. *Neuron* 53, 9–16.
5. Zorzi, M., Priftis, K., and Umiltà, C. (2002). Brain damage: neglect disrupts the mental number line. *Nature* 417, 138–139.
6. Bowers, D., and Heilman, K.M. (1980). Pseudoneglect - effects of hemispace on a tactile line bisection task. *Neuropsychologia* 18, 491–498.
7. Diekamp, B., Regolin, L., Gunturkun, O., and Vallortigara, G. (2005). A left-sided visuospatial bias in birds. *Curr. Biol.* 15, R372–R373.
8. Gobet, S.M., Calabria, M., Farne, A., and Rossetti, Y. (2006). Parietal rTMS distorts the mental number line: Simulating 'spatial' neglect in healthy subjects. *Neuropsychologia* 44, 860–868.
9. Longo, M.R., and Lourenco, S.F. (2007). Spatial attention and the mental number line: Evidence for characteristic biases and compression. *Neuropsychologia* 45, 1400–1407.
10. Brugger, P. (1997). Variables that influence the generation of random sequences: an update. *Percept. Motor Skills* 84, 627–661.
11. Nicholls, M.E.R., and Roberts, G.R. (2002). Can free-viewing perceptual asymmetries be explained by scanning, pre-motor or attentional biases? *Cortex* 38, 113–136.
12. Schindler, I., and Kerkhoff, G. (1997). Head and trunk orientation modulate visual neglect. *Neuroreport* 8, 2681–2685.
13. Meador, K.J., Loring, D.W., Bowers, D., and Heilman, K.M. (1987). Remote memory and neglect syndrome. *Neurology* 37, 522–526.
14. Kinsbourne, M. (1972). Eye and head turning indicates cerebral lateralization. *Science* 176, 539–541.
15. Wilson, M. (2002). Six views of embodied cognition. *Psychon. Bull. Rev.* 9, 625–636.

Department of Neurology, Neuropsychology Unit, University Hospital Zurich, CH-8091 Zurich, Switzerland.
E-mail: peter.brugger@usz.ch

Experiments with robots explain synchronized courtship in fiddler crabs

Leeann T. Reaney, Rachel A. Sims, Stephen W.M. Sims, Michael D. Jennions and Patricia R.Y. Backwell

Male fiddler crabs (*Uca mjoebergi*) produce highly synchronized courtship waves. Is this a cooperative behaviour because females preferentially approach groups that wave synchronously? Or is it a competitive behaviour because of female choice for males that wave first, with the resultant selection on males generating synchrony as an epiphenomenon [1]? To find an answer we used robotic male crabs to measure female mating preferences. We show that females do not prefer males waving in synchrony, but they strongly prefer males that wave first ('leaders'). Synchrony therefore appears to be a by-product of competitive interactions between males.

Synchronized male sexual advertisement is a spectacular phenomenon occurring in several taxa. It almost always involves acoustic or bioluminescent signals [1]. There are two main explanations for its occurrence. First, synchronization is cooperative if females prefer synchronous groups so that all male participants potentially benefit. This could explain synchronized bioluminescence for long-range attraction by fireflies. Second, when two acoustic signals are produced in rapid succession, receivers often respond more strongly to leaders than followers ('precedence effect') [2,3]. Game theory modelling shows that selection on signal timing to increase the likelihood of leadership generates synchrony as an epiphenomenon. This mechanism can successfully explain synchronous acoustic choruses [4,5]. The precedence effect has, however, only been demonstrated for acoustic signals and the proximate mechanisms implicated

(for example, call masking) are not necessarily applicable to other sensory modalities [2,3].

To date, we lack direct evidence that a standard visual signal based on reflected light that is produced synchronously by courting males has arisen either because of a female preference for synchronous groups or through a precedence effect. In fiddler crabs, however, where neighbouring males wave their claws in tight synchrony to attract females, there is a positive correlation between leadership and attractiveness [6]. This suggests that the precedence effect promotes synchrony, but experimental evidence for this is lacking [7]. We therefore built four robotic fiddler crabs that resemble courting males (see Supplemental data available on-line with this issue) to investigate synchrony in *U. mjoebergi* in Darwin, Australia. Mate-searching females approach a cluster of males and enter one male's burrow. If suitable, they stay and mate [8]. For 24 females we measured wave synchrony between the visited male and his nearest neighbour as $\alpha = [(t_n - t_v)/T_v] \times 360^\circ$ ($t_n - t_v$ = time between wave onset by the neighbour and visited male; T_v is the interval between successive waves by the visited male) [4]. Synchrony is perfect if $\alpha = 0^\circ$ or 360° and there is perfect alternation if $\alpha = 180^\circ$. In *U. mjoebergi* there is tight synchrony ($\alpha = 5.2^\circ \pm 6.8^\circ$ s.e.; Rayleigh's test, $Z = 17.1$, $P < 0.0001$) (Figure 1A; see also Supplemental Movie S1).

Mate choice trials were conducted in the field. In each experiment one pair of robotic crabs was set up 40 cm from a second pair (robots 5 cm apart within pairs). All robots had identical wave rates. We then captured a burrowless female and placed her under a cup equidistant between the pairs. After acclimation, we released her and noted which robot she approached. Females exhibited behaviour characteristic of mate choice during their approach, such as typical jerky movements (Supplemental Movie S2). We only scored a trial if the female saw all four robots wave at least twice before choosing. *P*-values are from binomial tests ($n = 40$ females/experiment).

We first offered females a choice between a synchronous pair ($\alpha = 0^\circ$)

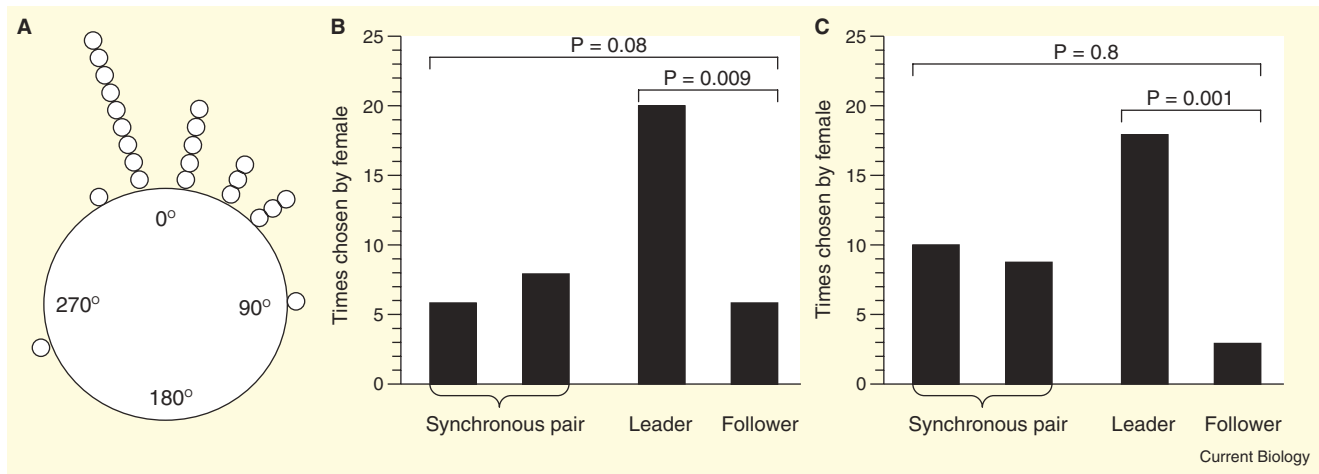


Figure 1. Synchronous waving and female choice in fiddler crabs.

(A) Natural courtship wave synchrony (α values; see text) between a female-visited male and his nearest neighbours ($n = 24$ females). (B) Proportion of females that approached the synchronously or asynchronously waving pair ($n=40$ females), for the asynchronous leader-follower pair $\alpha=60^\circ$. (C) As for (B) but $\alpha=30^\circ$.

and a pair producing alternating waves ($\alpha = 180^\circ$). Females did not prefer the synchronous pair (19 versus 21; $P=0.88$). However, alternation in one pair results in a leader–follower relationship *between* pairs: each male in the synchronous pair is a follower for one male of the asynchronous pair and a leader for the other male of the asynchronous pair ($\alpha=90^\circ$ and 270°). We therefore gave females another choice ensuring perfect three-way alternation between a synchronous pair and two asynchronous males (see Supplementary data for graphical representation of wave timing). Again, females did not prefer the synchronous pair (18 versus 22; $P=0.64$). This design, however, always creates a leader and follower *within* the asynchronous pair ($\alpha = 120^\circ$). Interestingly, females that approached the asynchronous pair significantly preferred the leader (17 versus 5; $P=0.017$). In two subsequent experiments we ensured that one male in the asynchronous pair had waves that alternated with those of the synchronous pair, but reduced the within-pair leader–follower relationship to $\alpha=60^\circ$ then $\alpha=30^\circ$. Females did not prefer synchrony ($P=0.08$ and 0.88), but still preferred the leader whenever they approached the asynchronous pair ($P=0.009$ and 0.001) (Figure 1B,C).

Our experiments show that, despite appearances, synchrony is not favoured because male

U. mjoebergi cooperate to wave in synchrony. The trend was for females to more often approach an asynchronous pair (pooled data: $P=0.13$). However, females that approached a leader–follower pair strongly preferred the leader. This preference was equally strong when α was 120° , 60° or 30° ($\chi^2=0.67$, $P=0.71$). The degree of synchrony (α) at which females no longer prefer or detect leaders is unknown but must be $<30^\circ$. Interestingly, real males whose burrows were visited by mate-searching females were not leaders relative to their neighbour (Wilcoxon test, $Z=1.23$, $P=0.22$, $n=24$). This suggests that highly synchronised waving by males in nature ($\alpha \approx 5^\circ$) has eliminated a readily detectable precedence effect.

The most plausible explanation for synchrony is that it is an epiphenomenon of selection on males to adjust signal timing because females prefer leaders [1,4,5]. Previously, explanations that relied on this ‘precedence effect’ only seemed relevant for acoustically signalling species [2,3]. Here we have shown experimentally that this effect is also relevant for a visual signal based on reflected light. Our findings raise broader questions about the neurobiology and psychophysics of the precedence effect. Specifically, is there a simple biological constraint (akin to the refractory period after perception of an acoustic signal), or has there

been selection on females to prefer leaders because leadership conveys fitness-enhancing information about male quality?

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Supplemental data

Supplemental data are available at <http://www.current-biology.com/cgi/content/full/18/2/R62/DC1>

References

- Greenfield, M.D. (2005). Mechanisms and evolution of communal sexual displays in arthropods and anurans. *Adv. Stud. Behav.* 35, 1–62.
- Wallach, H., Newman, E.B., and Rosenzweig, M.R. (1949). The precedence effect in sound localization. *Am. J. Psychol.* 62, 315–336.
- Litovsky, R.Y., Colburn, H.S., Yost, W.A., and Guzman, S.J. (1999). The precedence effect. *J. Acoust. Soc. Am.* 106, 1633–1654.
- Greenfield, M.D. and Roizen, I. (1993). Katydid synchronous calling is an evolutionary stable outcome of female choice. *Nature* 364, 618–620.
- Greenfield, M.D., Tourtellot, M.K., and Snedden W.A. (1997). Precedence effects and the evolution of chorusing. *Proc. R. Soc. Lond. B* 264, 1355–1361.
- Backwell, P., Jennions, M., Passmore, N., and Christy, J. (1998). Synchronised courtship in a fiddler crab. *Nature* 391, 31–32.
- Backwell, P.R.Y., Jennions, M.D., Christy, J.H. and Passmore, N.I. (1999). Female choice in the synchronous waving fiddler crab, *Uca annulipes*. *Ethology* 105, 415–421.
- Reaney, L.T., and Backwell, P.R.Y. (2007). Temporal constraints and female preference for burrow width in the fiddler crab, *Uca mjoebergi*. *Behav. Ecol. Sociobiol.* 61, 1515–1521.

School of Botany and Zoology, Australian National University, Canberra, ACT 0200, Australia.

E-mail: Michael.Jennions@anu.edu.au