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DUNLIN CHORUS LINE

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The chorus-line hypothesis of manoeuvre coordination in avian flocks

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Thousands of birds flying together at high speeds are able to execute abrupt manoeuvres with such precise coordination that some investigators have postulated that 'thought transference'[1] or electromagnetic communication[2] must be taking place. Recently, Davis proposed that coordination is achieved by a 'threshold' number of birds executing 'preliminary movements' which signal to the flock that a turn is imminent[3]. Here I show by analysis of film of dunlin (*Calidris alpina*) flocks that a single bird may initiate a manoeuvre which spreads through the flock in a wave. The propagation of this 'manoeuvre wave' begins relatively slowly but reaches mean speeds three times higher than would be possible if birds were simply reacting to their immediate neighbours. These propagation speeds appear to be achieved in much the same way as they are in a human chorus line: individuals observe the approaching manoeuvre wave and time their own execution to coincide with its arrival.

The 'chorus-line' hypothesis suggests that manoeuvres are initiated by any bird executing a manoeuvre towards the flock and that subsequent coordination is achieved through visual communication. This leads to the prediction that execution of the manoeuvre by neighbours of the initiator will be delayed by at least their own reaction time but, further away, response times should fall as birds are able to estimate the arrival of the approaching manoeuvre wave. Films taken of human chorus lines indicate that rehearsed manoeuvres, initiated without warning, propagate from person to person approximately twice as fast (107.7 ± 6.8 ms, $n = 3$) as the 194-ms human visual reaction time[4].

Coordinated manoeuvres (defined as those in which interbird response times were faster than laboratory measured reaction times) were investigated by field observations and analyses of 2,000 ft of slow-motion (50 frames s^{-1}) 16-mm film taken of dunlin flocks at Puget Sound, Washington. Manoeuvres were either natural or were induced artificially by shooting an arrow near an airborne flock. Twenty-two coordinated and four non-coordinated manoeuvres, chosen for clarity of detail, were analysed frame-by-frame. Startle reaction times to a light flash were measured in the laboratory using previously reported methodology[5].

In films where initiators and all neighbours were discernible, coordinated manoeuvres were initiated by one or a few individuals (one initiator, $n = 9$; two, $n = 3$; three, $n = 2$; $>$three, $n = 0$). Birds were considered initiators when they began the manoeuvre before the rest of the flock. In all cases coordinated manoeuvres were initiated by birds banking towards the flock ($n = 22$). When flock members turned away from the flock, the flock either did not follow ($n = 16$), or did so at speeds too low to qualify as a coordinated manoeuvre (84.8 ± 15.5 ms, $n = 4$). Manoeuvres always propagated through the flock in a wave radiating from the initiation site. These waves were observed to travel along every major axis (including back to front), indicating that manoeuvres may be initiated from any region of the flock. They had a mean propagation time from neighbour to neighbour of 14.6 ± 6.7 ms ($n = 9$), considerably lower than the laboratory measured startle reaction time of 38.3 ± 3.1 ms ($n = 110$). Therefore, manoeuvres propagate through flocks in waves travelling at speeds nearly three times faster than possible if flock members are following the actions of adjacent neighbours. However, the first neighbours to respond to the initiator required 67 ± 24 ms ($n = 14$). This mean propagation time from initiator to neighbours was significantly slower than both the mean manoeuvre propagation time (14.6 ms, $P < 0.0001$), and the mean species reaction time (38.3 ms, $P < 0.0001$; Wilcoxon rank sum test).

These results show that manoeuvres initially propagate more slowly than the birds' reaction time and then accelerate to high propagation speeds, as predicted by the chorus line hypothesis. Alternative hypotheses make no explicit predictions about the form of propagation, but imply that manoeuvres can occur in unison. No unison manoeuvres were seen. No preliminary movements which might signal that a turn is imminent[3] were seen, although such movements should be visible on film if they are to be visible to what is often thousands of tightly packed[6] flock members.

Flock members always appear to follow the lead of initiators banking towards the flock. This 'dictatorial' rule by initiators presumably prevents indecision and allows flocks to respond rapidly during attacks by birds of prey, which are a major source of mortality for flocking shorebirds[7]. Birds of prey usually direct their attack toward individuals isolated from the main flock[7,8], and this may well have exerted selection pressure for the evolution of coordinated manoeuvres.

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1. Selous, E. *Thought-transference (or what?) in Birds* (Constable, London, 1931).
2. Heppner, F. H. & Haffner, J. in *Biological and Clinical Effects of Low Frequency Magnetic and Electric Fields* (eds Llaurado, J. G., Sauces, A. Jr & Battocletti, J. H.) 147–162 (Thomas, Illinois, 1974).
3. Davis, J. M. *Anim. Behav.* **28**, 668–673 (1980).
4. Teichner, W. H. *Psychol. Bull.* **51**, 128–149 (1954).
5. Pomeroy, H. & Heppner, F. *Anim. Behav.* **25**, 720–725 (1977).
6. Major, P. F. & Dill, L. M. *Behavl Ecol. Sociobiol.* **4**, 111–112 (1978).
7. Page, G. & Whitacre, D. F. *Condor* **77**, 73–83 (1975).
8. Rudebeck, G. *Oikos* **3**, 200–231 (1951).

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