

## Two Eyes for an Eye: The Neuroscience of Force Escalation

Sukhwinder S. Shergill,<sup>1,2</sup> Paul M. Bays,<sup>1</sup> Chris D. Frith,<sup>1</sup> Daniel M. Wolpert<sup>1\*</sup>

Physical conflicts tend to escalate. For example, as tit-for-tat exchanges between two children escalate, both will often assert that the other hit him or her harder. Here we show that, in such situations, both sides are reporting their true percept and that the escalation is a natural by-product of neural processing.

Six pairs of naïve participants took part in a tit-for-tat experiment. Each member of a pair rested his or her left index finger in a molded support. A force transducer, which was attached to a lightweight lever of a torque motor, was placed on top of this finger (Fig. 1, inset). A trial was started by one torque motor producing a 0.25 N force on one participant's finger. Participants then took turns to press with their right index finger down for 3 s on the force transducer resting on the other's left index finger. They were instructed to apply the same force on the other participant that had just been exerted on them. Each participant was unaware of the instructions given to the other. In all cases, the forces escalated rapidly (Fig. 1A). Across the six pairs, there was a significant ( $F_{1,5} = 12.1$ ,  $P < 0.05$ ) average increase of 3.2 N over the eight

turns corresponding to a 38% mean escalation on each turn. The increase was also significant ( $P < 0.05$ ) within every pair of participants. Thus, force escalation occurs rapidly even under instructions designed to achieve parity.

To investigate the basis of the escalation process, we examined the perception of force in an additional 12 naïve participants tested individually. A torque motor applied a brief constant force to the tip of the participant's left index finger that was resting in a molded support. When participants were required to use their right index finger to match the perceived force, by pushing on their left index finger through the force transducer, they consistently overestimated the force required [Fig. 1B (•)]. This observation suggests that self-generated forces are perceived as weaker than externally generated forces of the same magnitude. This could arise from a predictive process (1–3) in which the sensory consequences of a movement are anticipated and used to attenuate the percepts related to these sensations. Such a mechanism removes some of the predictable

component of the sensory input to self-generated stimuli, thereby enhancing the salience of sensations that have an external cause (4–7). In a second condition, participants were required to reproduce the experienced force using their right index finger to move a joystick that controlled the force output of the torque motor. The active hand does not generate the force directly; the hand's movement is translated into a force through the torque motor. In this unusual situation, predictive mechanisms are not employed (8). When the force was generated via the joystick, the reproduced

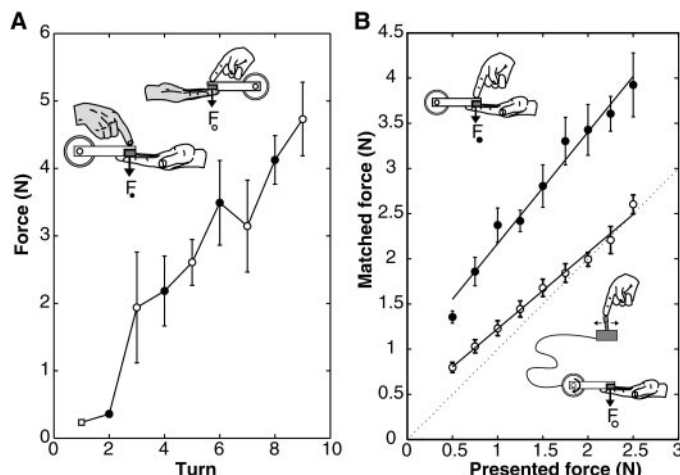
force matched the original force much more accurately [Fig. 1B (○)]. A regression analysis showed a significant increase in both the intercept ( $F_{1,11} = 18.1$ ,  $P < 0.01$ ) and slope ( $F_{1,11} = 25.7$ ,  $P < 0.001$ ) when the force was applied directly rather than via the joystick. The average increase across the 12 participants was 0.53 N (0.12 N, SE) for the intercept and 49% (9%, SE) for the slope.

The attenuation of self-generated forces occurred in our experiments even though accurate perception of force was the primary requirement of the task, suggesting that such attenuation is very unlikely to be mediated via attentional mechanisms. Previous studies have shown that sensory perception is attenuated in a moving arm or finger (9–11). Here we have shown substantial attenuation in the resting finger when the tactile stimulus is self-generated (12). Despite the stimuli being identical at the level of peripheral sensation, the perception of force is reduced by about a half when the force is self-generated. Force escalation can, therefore, be seen as a by-product of predictive sensory attenuation.

### References and Notes

1. W. Sperry, *J. Comp. Physiol. Psychol.* **43**, 482 (1950).
2. E. Von Holst, *Brit. J. Anim. Behav.* **2**, 89 (1954).
3. D. M. Wolpert, Z. Ghahramani, M. I. Jordan, *Science* **269**, 1880 (1995).
4. L. Weiskrantz, J. Elliot, C. Darlington, *Nature* **230**, 598 (1971).
5. G. Claxton, *Percept. Motor Skills* **41**, 335 (1975).
6. S. J. Blakemore, D. M. Wolpert, C. D. Frith, *Nature Neurosci.* **1**, 635 (1998).
7. G. Curio, G. Neuloh, J. Numminen, V. Jousmaki, R. Hari, *Hum. Brain Mapp.* **9**, 183 (2000).
8. S. J. Blakemore, S. J. Goodbody, D. M. Wolpert, *J. Neurosci.* **18**, 7511 (1998).
9. R. W. Angel, R. C. Malenka, *Exp. Neurol.* **77**, 266 (1982).
10. R. J. Milne, A. M. Aniss, N. E. Kay, S. C. Gandevia, *Exp. Brain Res.* **70**:569 (1988).
11. C. E. Chapman, M. C. Bushnell, D. Miron, G. H. Duncan, J. P. Lund, *Exp. Brain Res.* **68**, 516 (1987).
12. The perception of force in the relaxed finger is mediated through mechanoreceptors. In the second group of participants, we also examined a condition in which they actively flexed their left finger during force presentation and matching so that afferents from the muscles and joints could also contribute to force perception. Attenuation in this contracted condition was not significantly different from that of the relaxed condition.
13. We thank J. Ingram for technical assistance and R. Flanagan for comments. Supported by the McDonnell Foundation, the Human Frontiers Science Programme, and Wellcome Trust.

4 April 2003; accepted 8 May 2003



**Fig. 1.** (A) Force escalation in a typical pair (participant 1, solid circles; participant 2, empty circles; mean  $\pm$  SE across four trials). The initial force (white square) was generated on participant 1 by the torque motor. (B) Matching force generated using the right finger (solid circles) and joystick (white circles) as a function of the externally generated force (mean  $\pm$  SE across participants). Dotted line, perfect performance. On each trial, the torque motor generated a force between 0.5 and 2.75 N for 3 s (40 pseudo-randomized trials). Each participant experienced both conditions in a counterbalanced order (participant 1, gray hands and solid circles; participant 2, white hands and open circles; mean  $\pm$  SE across four trials).

<sup>1</sup>Institute of Neurology, University College London, Queen Square, London WC1N 3BG, U.K. <sup>2</sup>Institute of Psychiatry, De Crespigny Park, London, U.K.

\*To whom correspondence should be addressed, E-mail: wolpert@hera.ucl.ac.uk