needs to account for gravitational pull, but task-level control should be adaptive and ignore such static inputs. The neurobiology of this sort of parallel control architecture has yet to be fully worked out in any animal. Invertebrates display complex and robust behavioral equilibrium reflexes with extremely limited neural resources, a paradox which serves to experimentally highlight the underlying neural mechanisms.

Summary

We share a physical world with invertebrates, and as such we share the need to detect the effects of air and water currents, temperature, and gravity. Challenged by size and exhibiting tremendous evolutionary diversity, invertebrates exhibit some clever sensory solutions not available to us mammals. However, lessons learned from studies on invertebrate body senses also highlight convergent mechanisms for solving physical problems common to various taxa. Comparative research therefore holds value not just for more fully clarifying the diversity of solutions, but also for understanding how and why we humans arrived at our particular ones.

Further reading

Fraser, P.J. (2006). Review: Depth, navigation and orientation in crabs: Angular acceleration, gravity and hydrostatic pressure sensing during path integration. Mar. Fresh. Behav. Physiol. *39*, 87–97.

Frye, M.A., and Gray, J. (2005). Mechanosensory integration for flight control in insects. In: T. Christensen (ed), Methods in Insect Sensory Neuroscience, series Frontiers in Neuroscience, CRC Press, Boca Raton.

Gillespie, P.G., and Walker, R.G. (2001). Molecular basis of mechanosensory transduction. Nature *413,* 194–202.

Hengstenberg, R. (1993). Multisensory control in insect oculomotor systems. Rev. Oculomotor Res. *5*, 285–298.

Preuss, T., and Hengstenberg R. (1992). Structure and kinematics of the prosternal organs and their influence on head position in the blowfly Calliphora erythrocephala. J. Comp. Physiol. *171*, 483–493.

Sane, S.P., Dieudonne, A., Willis, M.A., and Daniel, T.L. (2007). Antennal mechanosensors mediate flight control in moths. Science *315*, 863–866.

Webb, B. (2004). Neural mechanisms for prediction: do insects have forward models? Trends Neurosci. *27*, 278–282.

Zill, S., Schmitz, J., and Büschges, A. (2004). Load sensing and control of posture and locomotion. Arthropod Struct. Dev. *33*, 273–286.

[1]Department of Biology, Case Western Reserve University, Cleveland, OH 44106-7080, USA. [2]Department of Physiological Science, University of California, Los Angeles, CA 90095-1606, USA.
E-mail: [1]jbender@case.edu, [2]frye@ucla.edu

Correspondences

Spontaneous planning for future stone throwing by a male chimpanzee

Mathias Osvath

Planning for a future, rather than a current, mental state is a cognitive process generally viewed as uniquely human. Here, however, I shall report on a decade of observations of spontaneous planning by a male chimpanzee in a zoo. The planning actions, which took place in a calm state, included stone caching and the manufacture of discs from concrete, objects later used as missiles against zoo visitors during agitated chimpanzee dominance displays. Such planning implies advanced consciousness and cognition traditionally not associated with nonhuman animals [1]. Spontaneous and unambiguous planning behaviours for future states by non-humans have not previously been reported, and anecdotal reports, describing single occasions, are exceptionally scarce [2–4]. This dearth of observations is arguably the main reason for not ascribing cognitive foresight to nonhuman animals [1]. To date, the surprisingly few controlled demonstrations of planning for future states by animals are experimentally induced behaviours in great apes [5–7] and corvids [8,9]. The observational findings in this report suggest that these laboratory results are not experimental artefacts, at least in the case of great apes.

Stone throwing toward a crowd of people has an instant and dramatic effect, and was a way to evoke reactions across the water moat that enclosed the chimpanzee. During the first three years during which this male chimpanzee held the dominant position, stone hurling was infrequent. This was probably because the outdoor island compound rarely contained stones immediately attainable in a display. In early June 1997, however, stone throwing increased dramatically, including several throws per display. This prompted zoo personnel to take precautionary measures.

One morning the chimpanzee island was swept, revealing five stone caches containing three to eight stones each, as well as individual stones between the caches, located along the shore facing the public area. Algae coating indicated that the stones originated from the adjacent waterbed (Figure 1). On subsequent days a caretaker placed herself in a blind to systematically observe the chimpanzee's behaviour. On five consecutive days, before the zoo opened, the chimpanzee gathered

Figure 1. Projectiles used in display. A concrete disc and two stones thrown at visitors in July 2008. The scale is in centimetres.

Figure 2. Displaying male chimpanzee. The male displays with a stone in his left hand. The forceful bipedal locomotion and the pilo-erection (hair on end) are signs of agitation.

stones from the water and placed them in caches. Later on each of these days, the stones were used as ammunition during displays (see Supplemental data available on-line for details).

In June 1998, the chimpanzee began to add pieces of concrete to the ammunition (Figure 1). Instead of restricting the stone gathering to the waterbed, he exploited the concrete rocks located at the centre of the island. In a sub-arctic zoo, concrete structures can be vulnerable to water entering and freezing in micro-cracks, partially detaching the surface layer. This is mostly invisible, but may be detected from a hollow sound when knocking on damaged areas. The chimpanzee was observed to gently knock on the concrete rocks, from time to time delivering harder blows to break off the detached surface section in discoidal pieces, and sometimes breaking these into further smaller fragments. These manufactured missiles were often transported to the caches at the shoreline.

Since the initial findings, caretakers have removed hundreds of caches. The gathering of stones has been observed on at least 50 distinct occasions, and the manufacturing of the concrete discs has been directly observed at least 18 times. However, concrete pieces were regularly present in the caches or individually along the shore.

In order for a behaviour to signal planning for a future state, the predominant mental state during the planning must deviate from the one experienced in the situation that is planned for. The above-described behaviour is clearly identifiable as planning for a future state. The chimpanzee has without exception been calm during gathering or manufacturing of the ammunition, in contrast to the typically aroused state during displays (Figure 2). The gathering and manufacturing has only been observed during the hours before the zoo opened, excluding potential triggering from the presence of zoo visitors. The delay between the gathering and the throwing of the stones is typically several hours. The chimpanzee has not been observed using stones or concrete in contexts other than throwing, and the behaviours have not been exhibited off-season when the zoo is closed and visitors are absent (50% of the yearly outdoor period is off-season). The purpose of the behaviours is further demonstrated by the fact that the discovered caches were always located at the shoreline facing the visitors' area; representing less than 25% of the island's circumference.

Planning, involving toolmaking, reveals a cognitive complexity not apparent in laboratory experiments. The production and use of concrete discs have been discovered or invented by the chimpanzee, as it had never been shown to him. The inferential chain, stretching from the detection of concrete hollowness to the offended visitors, comprises a noteworthy range of sequentially ordered advanced cognitive operations. This type of planning with tool making indicates a flexibility associated with mental pre-experience of an upcoming event [1]. The behaviours also hint at a parallel to human evolution, where similar forms of stone manipulation constitute the most ancient signs of culture. Finds as old as 2.6 million years suggest that hominins carried and accumulated stone artefacts on certain sites, presumably a case of future need planning [10].

Supplemental Data

Supplemental data are available at http://www.current-biology.com/supplemental/S0960-9822(09)00547-8.

Acknowledgments

I wish to thank the three senior chimpanzee caretakers for their time and devotion in the making of this report. I am grateful to Furuvik zoo that allowed research on such an unfavourable issue as stone-throwing animals. Thanks also to Tomas Persson for helpful comments on the manuscript.

References

1. Suddendorf, T., and Corballis, M. (2007). The evolution of foresight: what is mental time travel and is it unique to humans? Behav. Brain Sci. *30,* 299–351.
2. de Waal, F.B.M. (1982). Chimpanzee Politics: Power and Sex among Apes (London: Jonathan Cape).
3. Byrne, R. (1995). The Thinking Ape: Evolutionary Origins of Intelligence (Oxford: Oxford University Press).
4. Boesch, C., and Boesch-Acherman, H. (2000). The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution (Oxford: Oxford University Press).
5. Mulcahy, N., and Call, J. (2006). Apes save tool for future use. Science *312*, 1038–1040.
6. Osvath, M., and Osvath, H. (2008). Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: self-control and pre-experience in the face of future tool use. Anim. Cogn. *11*, 661–674.
7. Dufour, V., and Sterck, E.H.M. (2008). Chimpanzees fail to plan in an exchange task but succeed in a tool-using procedure. Behav. Proc. doi: 10.1016/j.beproc.2008.04.002.
8. Raby, C.R., Alexis, D.M., Dickinson, A., and Clayton, N.S. (2007). Planning for the future by western scrub-jays. Nature *445*, 919–921.
9. Correia, S.P.C., Dickinson, A., and Clayton, N.S. (2007). Western scrub-jays anticipate future needs independently of their current motivational state. Curr. Biol. *17*, 856–861.
10. Osvath, M., and Gärdenfors, P. (2005). Oldowan culture and the evolution of anticipatory cognition. Lund Univ. Cognit. Stud. *122*, 1–16.

Lund University Cognitive Science, Kungshuset Lundagård, 222 22 Lund, Sweden.
E-mail: mathias.osvath@lucs.lu.se