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## Integration of the Head and Forelimb in Bipedal Hominids

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Citation	Lieberman, Daniel E., Dennis M. Bramble, David A. Raichlen. 2007. Integration of the head and forelimb in bipedal hominids. ICVM-8 abstracts. Journal of Morphology 268(12): 1099.
Published Version	<a href="https://doi.org/10.1002/jmor.10589">doi:10.1002/jmor.10589</a>
Accessed	February 17, 2015 4:14:33 PM EST
Citable Link	<a href="http://nrs.harvard.edu/urn-3:HUL.InstRepos:2766653">http://nrs.harvard.edu/urn-3:HUL.InstRepos:2766653</a>
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Integration of the Head and Forelimb in Bipedal Hominids  
Daniel E. Lieberman, Dennis M. Bramble, David A. Raichlen

**Abstract:**

Integration, a fundamental property of organisms, occurs via multiple mechanisms and for diverse reasons. Although there has been substantial work on the genetic and epigenetic mechanisms by which developmental integration occurs, we have less of an understanding of the evolutionary relationships between functional and developmental integration. In this respect, human evolution provides an interesting test case. In quadrupedal mammals, there is considerable functional integration among and between the limbs, but little functional integration between the limbs and the skull. The evolution of bipedalism in hominids, however, provided new opportunities for novel forms of integration by emancipating the forelimbs from any major role in locomotion. Here we consider how the forelimb and head become increasingly integrated in the genus *Homo* because of the biomechanical challenges of running. While the arm and the head interact little during walking, we have found that, during running, the stance side arm acts as a counterbalance to the head, stabilizing it against impulsive pitching forces generated by the heel strike transient. Moreover, the functional properties of this linkage may have driven several developmental changes in the proportions of the arm and the anatomy of the shoulder girdle during human evolution. Thus, evolutionary changes in arm and head morphology during human evolution may be more integrated than previously considered.