dient constraint. For example, the disparity gradient constraint implies that a single image component in one eye cannot be fused at one moment with more than one component in the other eye. Such "multiple fusion" has been suggested as one explanation of depth perceived in Panum's limiting case (*5*). This stereogram may be constructed by presenting a single dot to one eye and a pair of dots to the other. In the nomenclature of Fig. 1, $\Theta_r = \Theta_\ell = R_\ell = 0$. Thus, $d_b = R_r$, $R_b = R_r/2$, and the gradient $d_b/R_b = 2$ is roughly twice as large as the limit we observed, so multiple fusion cannot occur.

The disparity gradient limit for fusion also implies that fusion space cannot "fold back" on itself when two or more objects occur at the same vertical level in the visual field. That is, fusion is not possible if the left-to-right order of the object images is reversed in one eye with respect to the other. Simple geometry will confirm that in this case, $d_b/R_b > 2$, which is outside the bounds for fusion.

We have found that fusion is never obtained when the disparity gradient exceeds a critical value of approximately 1° of disparity per degree of dot separation. Thus, diplopia occurs even for dots with disparities well within the classical Panum's fusional area whenever the gradient limit is exceeded. It is this failure of fusion under normally favorable conditions that most clearly demonstrates the critical role of object interactions in fusion. It seems that nearby objects "warp" the fusional space, creating forbidden zones in which changes in disparity are too steep for fusion.

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4. C. W. Tyler [*Vision Res.* **15**, 583 (1975)] has examined fusion when vertical disparity changes across horizontal positions. These results should not be confused with ours, in which the disparities are always horizontal. He also studied vertical line stereograms wiggling sinusoidally or in square-wave fashion and failed to observe disparity scaling for the latter (see his figure 9A).
5. K. N. Ogle [in *The Eye*, H. Davson, Ed. (Academic Press, New York, 1962), vol. 4, p.374] suggested that multiple fusion could account for depth in Panum's limiting case if disparities fall in Panum's fusional area. However, L. Kaufman and B. Lane [*Invest. Ophthalmol. Suppl.* *174* (1979)] argued that depth is due to eye vergence rather than multiple fusion.

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Telemetered Electromyography of Forelimb Muscle Chains in Gibbons (*Hylobates lar*)

Abstract. *Electromyographic studies of brachiation in the gibbon controvert deductions, based on dissection, about the purported functions of muscle chains in the hylobatid forelimb. Neither force conduction distally along the components of the chains nor simultaneity of muscular contraction occurs in brachiation. Rather, the unique structure of the forelimb is probably the result of evolved changes in the short head of biceps brachii to enhance its role as a forearm flexor.*

The acrobatic arm-swinging locomotion (brachiation) and highly specialized forelimb morphology of the lesser apes *Hylobates* (gibbon) and *Symphalangus* (siamang) have fascinated and puzzled natural historians, comparative anatomists, and anthropologists for more than a century (*1*, *2*). Brachiation dominates the locomotor repertoire of all lesser apes (*3*); and of all primates only these regularly engage in ricocheting brachiation (*2*-*4*), wherein the forelimbs act as propellant organs to hurl the animals across gaps in the forest canopy. Among the most prominent structural modifications in hylobatids are two sets of multiple-joint muscles that appear to be fused into two interacting chains: a ventral chain (pectoralis major to short head of biceps brachii to flexor digitorum superficialis) and a dorsal chain (latissimus dorsi to dorsoepitrochlearis to short head of biceps brachii to flexor digitorum superficialis). Deductive speculations about the function of these chains are based on dissection; they can be traced as far back as Sir Arthur Keith in the late 19th century (*5*), and have continued unabated to the present (*6*-*9*).

The ventral chain is purported to conduct the flexor force of the pectoralis major distally across shoulder, elbow, and wrist joints so that active or passive tension in this muscle results in automatic flexion of the forearm and fingers without requiring activity in the distal mem-

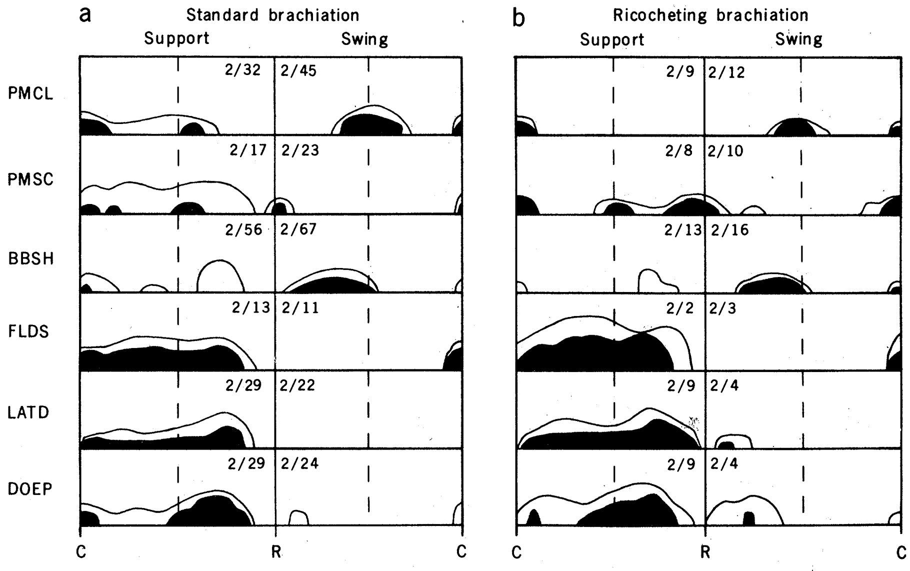

Fig. 1. Muscular activity during standard (a) and ricocheting (b) brachiation in *Hylobates lar*. Muscular components of the chains include pectoralis major pars clavicularis (*PMCL*), pectoralis major pars sternocostalis (*PMSC*), short head of biceps brachii (*BBSH*), flexor digitorum superficialis (*FLDS*); latissimus dorsi (*LATD*), and dorsoepitrochlearis (*DOEP*). Contact and release of the dowels are indicated by *C* and *R*, respectively; the dashed lines denote the middle of each phase of brachiation. The first number in each box refers to the number of individuals; the second, to the number of phase cycles counted (*10*). Blackened regions indicate highly consistent activity occurring at least 67 percent of the time in both animals; enclosed white regions, frequent but not consistent activity occurring at least 67 percent of the time in one subject or 33 percent of the time in both subjects. The height of each blackened or enclosed region indicates the relative amplitude of activity. Activity in a proximal member of the ventral chain (pectoralis major pars sternocostalis) was recorded at the moment of release—as the fingers were extending. Activity observed in proximal elements of the chains during the remainder of the swing phase was not associated with digital flexion. The activity of the flexor digitorum superficialis in the support phase (to establish a stable grip) and of the biceps brachii in the swing phase (to produce elbow flexion and thereby reduce the moment of inertia) demonstrates that, for these purposes, the animal does not rely on force conduction from more proximal muscles.

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bers of the chain (6–8). Contraction of proximal muscular elements in the dorsal chain is hypothesized to produce elbow and digital flexion by a similar mechanism of force conduction (5, 8). It is also suggested that simultaneous contraction of the muscles of the dorsal chain could prevent bowstringing the tendon of origin of the short head of the biceps brachii (6). One might apply similar reasoning to both chains by proposing that shunts of stress between muscles reduce the amount of tendon that must be stretched before useful force can be delivered. We conducted telemetered electromyographic studies (10) of the locomotion of the white-handed gibbon (*H. lar*) in order to evaluate the hypothesized functions of the ventral and dorsal muscle chains. Our findings do not substantiate the previous hypotheses, and indeed suggest that the chains are not functional units.

Telemetered electromyography permits the monitoring of muscle activity in alert animals as they move freely and naturally—without the interference of wires running to a recording device. Two adult *H. lar* (one male and one female) were encouraged to brachiate along a 7.3-m ladder suspended horizontally from the roof of a large enclosure (7.3 by 3.7 by 2.7 m). The crosspieces were wooden dowels (2.8 cm in diameter) placed every 40 cm. For purposes of analysis, hylobatid locomotion was divided into its two principal modes: standard brachiation (low to moderate speeds, with full body rotation) and ricocheting brachiation (aerial floating phases between handholds). After palpation of the muscles, bipolar fine-wire electrodes were inserted; correct placement was confirmed for each muscle by low-amperage back-stimulation (11). When each muscle of an anesthetized animal was back-stimulated, the movement observed was restricted to the joints crossed by that muscle alone.

We found that the patterns of muscle activity in standard and ricocheting brachiation are basically similar (Fig. 1), and controvert the hypothesis of force conduction distally along the elements of the chains. The activity by the sternocostal pectoralis to initiate the swing phase consistently occurred as the fingers extended to release their grasp of a support, rather than while they were flexing. Furthermore, no visible flexion of the fingers accompanied activity in any of the proximal elements of either chain during the remainder of the swing phase. Digital flexion prior to contact with a dowel was actively initiated by the flexor digitorum superficialis before electrical activity was observed in any of the proximal elements of either chain. The continuous and consistent activity by the flexor digitorum superficialis during the support phase (for establishing a stable grip), and the contraction of the biceps brachii during the swing phase (to produce elbow flexion and thereby reduce the moment of inertia) demonstrate that, for these purposes, the animal is unable to rely on force conduction from active or passive tension in more proximal elements.

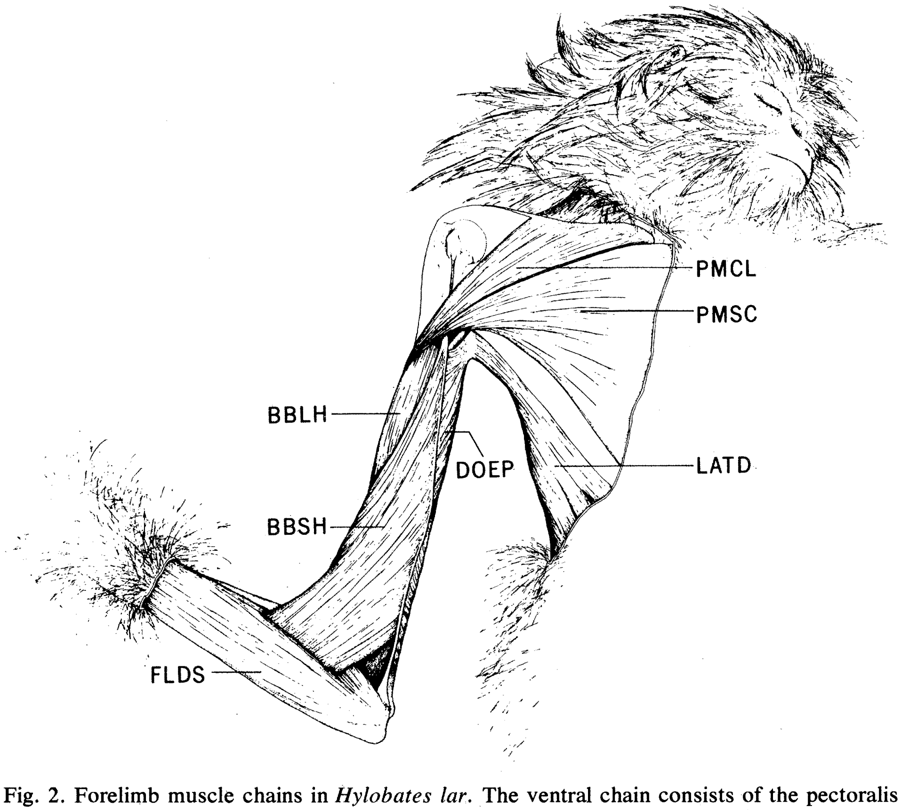

Fig. 2. Forelimb muscle chains in *Hylobates lar*. The ventral chain consists of the pectoralis major (clavicular and sternocostal portions), the short head of the biceps brachii, and the flexor digitorum superficialis. The dorsal chain consists of the latissimus dorsi, the dorsoepitrochlearis, the short head of the biceps brachii, and the flexor digitorum superficialis. (For abbreviations, see the legend to Fig. 1.) Note the slender tendon of origin of the short head of the biceps brachii from the lesser tuberosity of the humerus and the extensive origin of this head from the medial intermuscular septum (into which the dorsoepitrochlearis inserts in hylobatids and various other primates). The portion of the short head arising from the tendon inserts distally with the long head of the biceps brachii (*BBLH*) into the bicipital tuberosity of the radius. The additional fibers arising from the intermuscular septum insert into the interfascicular septa of the flexor digitorum superficialis and have an improved leverage for forearm flexion.

Our data for both modes of brachiation show that swing-phase activity in the biceps brachii occurs without synchronous recruitment of the dorsoepitrochlearis. This discredits the proposal that the link between the dorsoepitrochlearis and the short head of the biceps brachii is causally related to the requirement that the former muscle contract simultaneously with the latter to prevent bowstringing of the short head's tendon. Moreover, in the support phase, the dorsoepitrochlearis clearly plays a role independent of that of the short head of the biceps brachii. In general, the temporal spacing of electrical activity in the components of each chain cannot be construed as evidence for phasic simultaneity among these muscles in either phase of brachiation.

We conclude that the previous hypotheses about the apparent functional nature of the chains are fundamentally incorrect. We discovered no evidence supporting either the notion of force conduction from proximal to distal elements or the notion of phasic simultaneity during brachiation. Like Grönroos (12) in 1903, we regard the anatomical modification of the short head of the biceps brachii in hylobatid apes (Fig. 2) as the key to understanding its relation to the other muscles and the resultant impression of muscular chains. The potential action of the short head across the shoulder is effectively eliminated by the transfer of its tendon of origin from the coracoid process of the scapula to the lesser tuberosity of the humerus. A secondary attachment of the tendon of the pectoralis major onto the slender tendon of the short head probably shunts tensile stress from the latter and thereby relieves the proximal osseotendinous junction of the contracting short head. The portion of the short head arising from this tendon consists of long parallel fibers that insert distally with the long head of the biceps brachii into the bicipital tuberosity of the radius.

In addition, it is clear that the short head has acquired an extensive origin from the medial intermuscular septum of the arm. The increase in the number of muscle fibers implies a necessity for a larger area of insertion independent of the bicipital tuberosity. The distal insertion of these added fibers into the interfascicular septa of the flexor digitorum superficialis serves to increase the attachment area at the same time that it improves the leverage for forearm flexion (*13*). The origin of the dorsoepitrochlearis from the tendon of insertion of the latissimus dorsi, and its insertion into the medial intermuscular septum and medial epicondyle of the humerus, are not unique to hylobatid apes, but occur in various other anthropoid primates (*14*). However, due to the origin of the short head from the medial intermuscular septum in gibbon and siamang, the dorsoepitrochlearis must share this attachment site. The appearance of a dorsal chain is merely a by-product.

Since we believe that the unique structure of the hylobatid forelimb is the direct result of enlargement and other modification of the short head of the biceps brachii, we sought to identify behaviors in our gibbons that consistently recruit this muscle at its maximum level (as determined by periods of greatest electrical activity). In other words, we tried to determine when mechanical demands on the short head are at their peak in normal hylobatid locomotion. Our experiments revealed that such maximum bursts occur during especially rapid and forceful hoisting and are frequently associated with the initiation of ricocheting brachiation, at which time a powerful impulse is generated that often propels the animal above the level of its previous handhold (*2, 3*).

We regard these behaviors as uniquely hylobatid in their frequency and context, and as the probable selective forces behind (i) the shift in the origin of the short head of the biceps brachii (eliminating its dynamic action across the shoulder), (ii) the increase in the number of its fibers (creating greater flexor force), and (iii) the new insertion site into the interfascicular septa of the long digital flexors (providing improved mechanical advantage). Together, these adaptations led to morphological, not functional, muscle chains.

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Suprathreshold Processing of Complex Visual Stimuli: Evidence for Linearity in Contrast Perception

Abstract. *Magnitude estimation experiments show that perceived contrast for both sine and square waves is a linear function of stimulus contrast. The suprathreshold sine:square ratio required for equal perceived contrast derived from these data was verified by contrast matching experiments. These findings imply a high degree of linearity in suprathreshold visual processing of contrast.*

The question whether spatial information is processed approximately linearly by the visual system has importance for the selection of assumptions and techniques used to explain how objects are perceived. Linear processing allows the use of well-defined and easily implemented mathematical techniques, whereas nonlinear processing increases analytical complexity.

Campbell and Robson demonstrated linear processing of spatial vision at threshold (*1*). They found that, for spatial frequencies above 1 cycle/deg, the threshold for a sine-wave grating was higher than that for a square-wave grating by a factor of $4/\pi$, or 1.27. Since the fundamental Fourier component is the largest one in the spectrum of a square wave, having an amplitude 1.27 times the peak-to-peak amplitude of the square wave (*2*), they hypothesized that it mediates detection of the square wave.

At low spatial frequencies, Campbell and Robson found that (i) the fundamental did not mediate detection of the

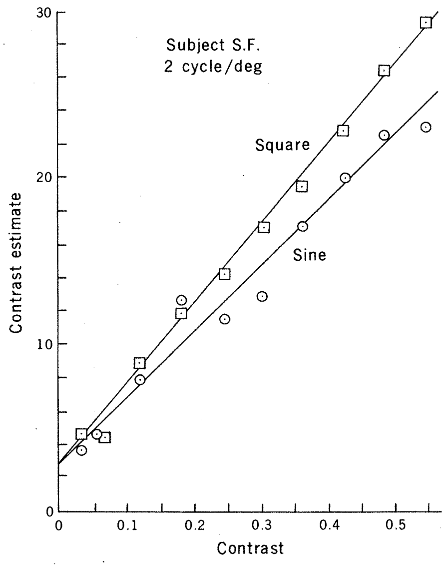

Fig. 1. Typical magnitude estimation data for the sine- and square-wave gratings. The contrast estimate axis represents the number assigned to the stimulus by the subject to estimate its contrast. The contrast axis represents the physical contrast of the stimulus as defined in the text. The lines through the data are least-square regressions.