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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References and Notes

1. W. Vrolik, *Recherches d'Anatomie Comparée sur le Chimpanse* (Johannes Miller, Amsterdam, 1841); J. H. F. Kohlbrügge, *Muskeln und Periphere Nerven des Genus Hylobates* (Brill, Leiden, Holland, 1890); F. K. Jouffroy and J. Lessertisseur, *Mammalia* **24**, 93 (1960); R. H. Tuttle, *Gibbon Siamang* **1**, 137 (1972).
2. O. zur Stassen, Ed., *Brehm's Tierleben: Allgemeine Kunde des Tierreichs* (Bibliographisches Institut, Leipzig, Germany, 1896); C. R. Carpenter, *Comp. Psychol. Monogr.* **16**, 1 (1940); J. O. Ellefson, *Gibbon Siamang* **3**, 1 (1974); J. G. Fleagle, *Malays. Nat. Hist. J.* **30**, 45 (1977).
3. J. G. Fleagle, *Folia Primatol.* **26**, 245 (1976); S. P. Gittins, thesis, University of Cambridge (1979).
4. R. H. Tuttle [*J. Morphol.* **128**, 309 (1969)] coined the term "richochetal brachiation" in reference to the saltatory bimanual locomotion of hylobatid apes.
5. A. Keith, *J. Straits Br. R. Asia Soc.* **23**, 77 (1891).
6. A. B. Howell and W. L. Straus, *Proc. U.S. Natl. Mus.* **80**, 1 (1931).
7. R. A. Miller, *Am. J. Phys. Anthropol.* **17**, 1 (1932).
8. P. Andrews and C. P. Groves, *Gibbon Siamang* **4**, 167 (1976).
9. R. H. Tuttle, in *Phylogeny of the Primates*, W. P. Luckett and F. S. Szalay, Eds. (Plenum, New York, 1975), p. 447; *Yearb. Phys. Anthropol.* **20**, 491 (1977).
10. J. T. Stern, Jr., J. P. Wells, A. K. Vangor, J. G. Fleagle, *Yearb. Phys. Anthropol.* **20**, 498 (1977); R. L. Susman and J. T. Stern, Jr., *Am. J. Phys. Anthropol.* **50**, 565 (1979). Details of quantification of electromyographic activity and telemetry system specifications are provided by J. T. Stern, Jr., J. P. Wells, W. L. Jungers, A. K. Vangor, and J. G. Fleagle [*ibid.* **52**, 13 (1980)].
11. I. Engberg and A. Lundberg, *Acta Physiol. Scand.* **75**, 614 (1969); S. Rasmussen, A. K. Chan, G. E. Goslow, Jr., *J. Morphol.* **155**, 253 (1978).
12. H. Grönroos, *Abh. Kon. Preuss. Akad. Wiss. Berlin* (1903), p. 1.
13. J. T. Stern, Jr., *J. Biomech.* **7**, 411 (1974).
14. E. H. Ashton and C. E. Oxnard, *Trans. Zool. Soc. London* **29**, 553 (1963).
15. We thank M. Koltun and B. Korosh for their technical assistance with the animals, L. Betti for preparing the illustrations, and J. Kelly for secretarial assistance. Supported by NSF grants BNS 7683114A01 and BNS 7924070 and by NIH grant 5S07RR0577804.

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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

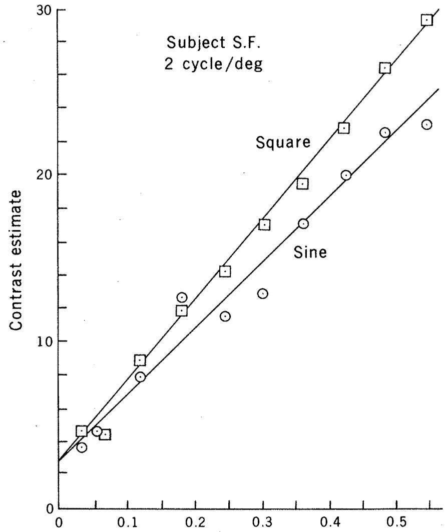

Fig. 1. Typical magnitude estimation data for the sine- and square-wave gratings. The contrast estimate axis represents the number assigned to the stimulus by the subject to estimate its contrast. The contrast axis represents the physical contrast of the stimulus as defined in the text. The lines through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

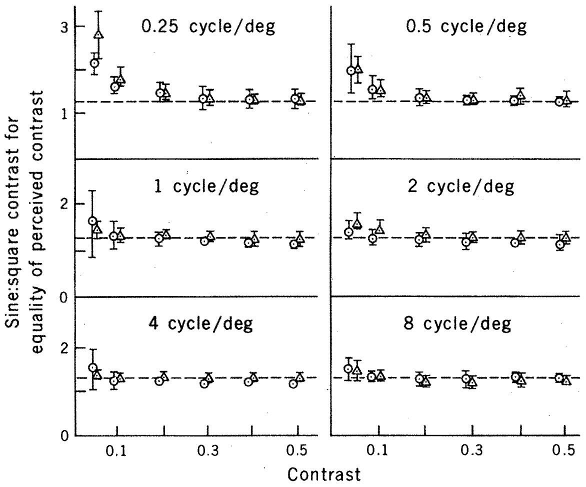

Fig. 2. Data points describing the sine : square ratio for both contrast matching (triangles) and magnitude estimation (circles) experiments. The horizontal dotted line is at amplitude $4/\pi$ in all panels. These data demonstrate that the ratio is equal to $4/\pi$ over a large range of contrasts and spatial frequencies.

square wave and (ii) the ratio of sine-wave to square-wave contrast thresholds increased monotonically up to at least a factor of 4 with decreasing spatial frequency. This phenomenon has not yet been explained, but it has been recently replicated by Howell and Hess (*3*). Whatever the final explanation of this phenomenon proves to be, it is evident that their model explains the behavior of the visual system at threshold over a wide range of spatial frequencies greater than about 1 cycle/deg.

Although these results are of great interest, the largest part of the human visual world exists above threshold. Therefore, it is important to determine how contrast is perceived at suprathreshold levels. Hamerly, Quick, and Reichert (*4*) and Cannon (*5*) have demonstrated by the technique of magnitude estimation that perceived contrast (or contrast sensation) is a linear function of stimulus contrast for sine-wave gratings. Although perceived contrast appears to be linear for these simple stimuli, the question of how various spatial frequency components of a complex stimulus interact above threshold is unknown. We compared the perceived contrast of square waves and sine waves at stimulus contrast (C) as high as 0.5 [$C = (L_{\max} - L_{\min})/(L_{\max} + L_{\min})$, where L = luminance].

Two different psychophysical methods were used to provide a cross-check on our results: contrast matching (class A) and magnitude estimation (class B) (*6*). Data were collected by both methods from three subjects at six spatial frequencies.

In the contrast matching experiment, subjects were required to adjust the contrast of a test grating until it appeared to match that of a 4 cycle/deg sine-wave reference grating set at one of five contrasts from 0.025 to 0.5. The test gratings were either sine waves or square waves of spatial frequencies from 0.25 to 8 cycle/deg. The split-screen display was presented on a specially designed video monitor with the mean luminance maintained at 3.5 footlamberts (12 cd/m^2) (*7*).

Contrast matches produced by all subjects for both sine and square waves were plotted to show matching contrast as a function of reference contrast and were fitted with linear regression lines. Values of r (correlation coefficient) for all regressions were typically .98 or greater. These data showed that square waves always required less contrast to match the reference sine wave than did sine waves of the same spatial frequency as the square wave.

The method of magnitude estimation required subjects to assign a number, proportional to the perceived contrast, to each stimulus presentation. Square- and sine-wave gratings of the same spatial frequency, with ten contrasts evenly spaced between 0.03 and 0.54, were presented in random order on the same apparatus and with the same luminance conditions used for the matching experiment. Stimuli were presented periodically for 2 seconds and followed by 8 seconds of uniformly illuminated screen. Estimated contrast values produced by one of the three subjects are illustrated in Fig. 1. Linear regression, used to fit the lines through the data points, produced r values of .98 or greater, as with the matching data.

Linearity of the relationship between perceived and stimulus contrast was observed for both sine- and square-wave gratings at all spatial frequencies tested. For single component stimuli (*4, 5, 8*), this behavior is in agreement with previously published data. These new data demonstrate that the perceived contrast of a square-wave grating is always greater than that of a sine wave of the same spatial frequency and contrast.

Using the regression lines of the magnitude estimation and contrast matching data of each subject, we calculated the ratio of sine-wave to square-wave contrast required to equate the perceived contrast of both stimuli. The calculations were performed at five levels of square-wave contrast, and the ratios were averaged across subjects at each spatial frequency (Fig. 2). Agreement between the results of magnitude estimation and contrast matching experiments is excellent for all contrasts and spatial frequencies studied. This agreement between two fundamentally different psychophysical techniques argues well for predominantly linear visual processing (*9*).

The suprathreshold data demonstrate that the sine:square ratio remains at approximately $4/\pi$ at all contrasts tested above 1 cycle/deg, behavior similar to the results of Campbell and Robson at threshold. The ratio decreases to near $4/\pi$ at contrasts above 0.2 for lower spatial frequencies. The combined results of both experimental methods indicate that perceived contrast of a square wave is directly proportional to the magnitude of its fundamental frequency component and is predominantly linear over a wide range of spatial frequencies and contrasts (*10*). Apparently, the higher harmonics do not contribute greatly to overall contrast perception. However, observers perceive the grating as being a square wave and having sharp edges. This perception implies that the visual system can simultaneously use the higher harmonics in parallel to gain information about the shape and degree of sharpness of a stimulus. This selection of various spatial frequency components for perception of different properties of the stimulus supports the filter theory of visual perception proposed by Ginsburg (*11-13*). The fundamental proposition of that theory is that visual perception may be structured from a hierarchy of filtered images of objects. Each one-to-two-octave-wide spatial filter (channel) activated by the spatial properties of an object provides a portion of the information about the object that can be attended to somewhat independently of the other information. General contrast information is provided by the filters that pass the lowest spatial frequency components of the object. Form detection and identification are provided by filters centered on the frequencies of a small number of low-frequency components. Fine detail is provided by filters tuned to higher frequency components. The magnitude estimation results and their corroboration by contrast matching fosters a cautious optimism that these spatial frequency filters behave almost linearly with contrast over the range studied. Therefore, simulations of a hierarchy of these filters may provide a good first approximation to many of the visual cues required for the perception of complex objects. Furthermore, linear modeling may be as useful for predictive modeling of suprathreshold phenomena as it has been at threshold.

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References and Notes

1. F. W. Campbell and J. G. Robson, *J. Physiol. (London)* **197**, 551 (1968).
2. The Fourier expansion of a square wave of contrast C, period T, and distance x given by the infinite series

$$C4/\pi\left(\sin\frac{2x}{T}+\frac{1}{3}\sin\frac{6x}{T}+\frac{1}{5}\sin\frac{10x}{T}+\cdots\right)$$

contains only odd harmonic components. The fundamental or first harmonic component has amplitude $4/\pi\ C$ (or $1.27\ C$) and therefore has a larger amplitude than the peak-to-peak amplitude of the square wave.
3. E. R. Howell and R. F. Hess, *Vision Res.* **18**, 369 (1978).
4. J. R. Hamerly, R. F. Quick, Jr., T. A. Reichert, *ibid.* **17**, 201 (1977).
5. M. W. Cannon, *ibid.* **19**, 1045 (1979).
6. G. S. Brindley, *Physiology of the Retina and Visual Pathway* (Arnold, London, 1970).
7. Our equipment limited the maximum luminance and contrast values used in this study. However, contrast matching studies at lower mean luminance levels support our findings.
8. J. J. Kulikowski, *Vision Res.* **16**, 1419 (1976).
9. We thank a referee for pointing out that the $4/\pi$ ratio obtained from the contrast match between the sine- and square-wave gratings does not by itself provide evidence of linear contrast transduction. Any nonlinear function operating at all spatial frequencies of contrast would produce that result. This is not true for the magnitude estimation results, however. The degree of linearity of perceived contrast (Fig. 1) cannot be due to any nonlinear transduction function. Since these data show the predicted $4/\pi$ ratio, the high linearity of perceived suprathreshold contrast is supported. Since the contrast matching results are similar, it is unlikely that there is any significantly different processing of contrast between the two techniques. Indeed, that these two dissimilar techniques produce similar results is important.
10. These results are not in agreement with the data of Hamerly, Quick, and Reichert (*4*) for the perceived contrast of two superimposed sine-wave gratings of frequencies f and $3f$. They reported a linear addition of perceived contrast when the two stimuli were presented simultaneously at contrasts above 0.05. Our square-wave results indicate that its higher harmonics do not add linearly to the fundamental. Further experiments are needed to determine the cause of this difference. D. Tolhurst [*J. Physiol. (London)* **226**, 231 (1972)] found adaptation effects with suprathreshold square-wave gratings that he attributed to inhibition between the fundamental and third harmonic frequencies. Our results suggest little or no such interaction under our experimental conditions.
11. A. P. Ginsburg, *IEEE Trans. Aerosp. Electron. Syst. 71-C-24 AES* (1971), p. 283.
12. ———, *Invest. Ophthalmol. Visual Sci. Suppl.* (1977), 16 (abstr.); *ibid.*, p. 123.
13. ———, thesis, University of Cambridge (1977); *Air Force Aerospace Medical Research Laboratory Rep. TR-78-129*, in press.

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Saccadic Eye Movements and Body Sway

Abstract. *Different conditions of moving retinal images show differential influences on postural stability. A surrounding pattern moved during steady fixation increases body sway, but similar image motions generated by voluntary saccades do not. Mechanisms for postural control do not respond to visual feedback during saccades. Analogous principles in saccadic suppression and space constancy are discussed.*

Maintaining a steady upright posture depends on a fine balance between opposing muscular actions. This balance is controlled reflexively in accord with sensory feedback from proprioceptive joint and muscle afferents, vestibular organs, and the visual system. When an imbalance of forces results in sway of the body, the head and eyes move with respect to the surroundings so that optical images move across the retinas (*1*). Feedback for the multiloop control of posture from this movement of the retinal image is useful for reducing slow body sways to which the other systems are not sensitive (*2*). One's steadiness while standing on one foot illustrates the stabilizing effect of visual feedback. Steadiness improves when surrounding objects are visible and is diminished by closing the eyes.

Although vision normally stabilizes posture, in restricted circumstances it provides "false" feedback. Motion of the retinal image analogous to that induced by sway can be imposed experimentally, as by coherent movement of the whole visual surroundings, and the false signal can evoke inappropriate countersway. We noted that similar motions of optical images across the retinas accompanied lateral sways or small horizontal saccadic eye movements. Can the eye movements cause a false feedback signal?

The processing of visual information during a saccadic eye movement is a classic question of perception. In the course of a saccade, the rapid motion of optical images across the retina should appear blurred as a result of temporal summation, yet the blur is seldom seen. Nor does one get the impression that the world moves when the gaze is redirected voluntarily (*Raumkonstanz* or space constancy). In terms of visual information transfer, the perception of blur and of motion is thought to be reduced significantly by loss of visual sensitivity (saccadic suppression) during the course of an eye movement. Studies of visual detection or acuity find reduced sensitivity accompanying saccades, and other visual functions such as target localization may be altered around the times of eye movements (*3*). To our knowledge, however, prior studies have not investigated postural stability—a context of spatial orientation that may interact with voluntary eye movements.

We reasoned that investigating body sway could contribute to our understanding of visual information processing during a saccade since the mechanisms that control sway are behaviorally and neurologically different from those governing the perceptual functions previously studied (*4*). We explored the possibility that visual aspects of body sway control are different in the presence of (i) the voluntarily produced motion of the retinal image accompanying a saccadic eye movement and (ii) an otherwise similar motion produced in the stationary eye by moving the visual surroundings.

Each subject viewed a large (180° horizontal by 120° vertical) grating pattern (0.08 cycle/deg) of gray and white vertical stripes. Near the center were two fixation lights separated horizontally by 4° of arc. The subject was instructed to fixate whichever light was illuminated. Voluntary saccades were directed by illuminating the lights alternately. Externally produced motions of the retinal image were generated while the subject fixated one light. For these, the grating pattern was moved horizontally through 4° of arc in 33 msec, closely approximating the average speed and duration of 4° saccades. Subjects stood on a rigid plate mounted on strain gages (stabilimeter). As the body's center of gravity shifted, forces exerted on each strain gage changed correspondingly. Subjects were instructed to stand on one foot to enhance lateral body sway (*5*).

Figure 1 presents the results, normalized with respect to individual differences. For normalizing, we took Fourier transforms of the lateral sways during 2-second sampling intervals and averaged the power spectra measured successively during each 16- or 32-second recording period ($N = 8$ or 16). These recording periods were either baselines, during which both the pattern and the eyes remained stationary, or tests, during which the conditions of interest were included. Our dependent measure was the ratio of test to baseline power spectra, namely, the gain in sway induced by a test condition. If the test conditions were without effect, the ratio