

increase in the speed. The response properties in Fig. 2B would be consistent with those of a cell exhibiting directional selectivity for sound sources moving from left to right at high velocities. There are other reports of directional sensitivity of auditory neurons using free-field or dichotic click stimuli, but the interaural phase sensitivities of the cells in these studies are not known (9).

The observation that most of the cells in our sample responded periodically at the rate of the beat frequency provides a possible neural correlate for the human psychoacoustic phenomenon of binaural beats (10). Human listeners report the sensation of beats up to $f \cong 60$ Hz. At very low beat frequencies ($f_b < 2$ Hz) subjects have reported a sensation of the tone moving in the head from one ear to another at the rate of f_b , in line with our interpretation that the binaural beat stimulus can simulate a moving sound source.

Although the binaural beat stimulus simulated the changing phase of the signals arriving at each ear for a naturally moving sound source, it cannot simulate the interaural intensity changes. These intensity differences are small for low-frequency sounds, but may still be a significant cue for sound localization. Furthermore, the pinna and external meatus play an important role in the natural situation. Nevertheless, the common symmetrical response to binaural beat stimuli (Fig. 2A) contrasts sharply with the more unusual asymmetrical responses when the frequencies to the two ears are interchanged (Fig. 2B), or when f_b is increased. This result at least implies a difference in sensitivity to direction or speed, or both.

Both the delay curves and the binaural beat period histograms suggest a mechanism for the center-surround organization described in the presumed avian homolog of the inferior colliculus of the owl (11). For most cells, the trough of the delay curve and period histograms is below the level of discharge that would be evoked by the contralateral ear alone (Fig. 1B). Hence there must be some inhibitory process that is active when the interaural phase relation corresponds to these troughs. When these curves are transformed into auditory space, one would expect the peaks to correspond to an excitatory receptive field with a limited spatial extent, bordered on both sides of the azimuth by inhibitory flanks.

As a technique for studying binaural interaction, the use of binaural beat stimuli is both efficient and practical. The strong correlation between response patterns generated by varying the interaural

delay and the binaural beat stimulus demonstrates the reliability of the method for studying interaural phase sensitivity while also providing information about the dynamic phase properties of the cells.

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6. By histological verification, all electrode tracks

were found to traverse the central nucleus of the inferior colliculus.

7. The peak phase angles were found by calculating the phase of the first Fourier coefficient of the period histograms (binaural beat stimuli) or averaged delay curves (interaural delay stimuli).
8. In reality, only one frequency will have a period perfectly matched to the maximum interaural delay. For example, for an interaural distance of 8.3 cm (that is, an interaural delay of 250 μ sec) and a sine wave of 2000 Hz (whose period is $2 \times 250 \mu$ sec), the sound will presumably just be lateralized to one ear when the stimuli are 180° out of phase. For $f < 2000$, $\phi = 0.5$ corresponds to a delay longer than 250 μ sec. During the time that the delay exceeds the physiological interaural delay, there will be an ambiguity as to the ear to which the source is lateralized. For $f > 2000$, ϕ will be 0.5 before the signal to one ear can lead the other by 250 μ sec, so the sound never completely lateralizes to that ear. At increasingly higher frequencies the source will move smaller distances from the midline.
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12. We thank T. Buunen for suggesting the use of the binaural beat stimulus for simulating a moving sound source and J. E. Rose, J. E. Hind, and our colleagues in the Department of Neurophysiology for critical reviews of our manuscript. Supported by NIH grants NS 12732 (to J. E. Hind) and EY02606 (to T. C. T. Y.).

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Moment of Inertia:

Psychophysical Study of an Overlooked Sensation

Abstract. *The distribution of mass in an object held in the hand, as described by its moment of inertia, is a fundamental and potent but largely unrecognized contributor to the object's "feel." A limited set of experiments has produced Weber fractions for human differential sensitivity to this property in the approximate range of 1/5 to 1/3, which is about ten times the Weber fraction reported for lifted weights.*

Designers of hand-held tools and commercial products must often improve the "feel" of the object as part of improving its overall performance. It is possible to enumerate and test many obvious properties contributing to feel, such as weight and balance, and sensitivities to them can be found in standard references or obtained by relatively simple psychophysical tests. However, a fundamental property of a body—its moment of inertia (I)—has been largely overlooked both as a decided contributor to the feel of an object and as a sensation in its own right (I).

The I of a body is a measure of its inertial resistance to rotational acceleration just as the mass (M) is a measure of inertial resistance to translational acceleration (2). Unlike M , however, I depends upon the axis chosen for the angular rotation and has the dimensions of mass \times (distance)². As the dimensions suggest, I can be increased by increasing M or by spreading the same mass out farther from the axis of rotation, just as the vari-

ance of a probability distribution increases as values depart from the mean. Therefore, with control over the shaping of a body of mass M , the three quantities, M , I , and CG (center of gravity), can be independent as long as no geometric restrictions are imposed. This independence still holds within limits as constraints such as length and diameter are placed on the body. Thus, two otherwise visually identical objects can have, for example, identical M and CG but different I values.

A simple experiment can demonstrate moment of inertia sensations. Tape a quarter to each end of a new unsharpened lead pencil, and, while holding it in the center between thumb and index finger in a horizontal position (for convenience), "twiddle" it like a rapid seesaw. Retape the quarters near the center of the pencil and twiddle it again. Now try to verbalize the difference between the two sensations.

Even subjects with scientific training attempting to describe the difference in

feel between two objects with different I values will almost invariably (and erroneously) respond in terms of differences in weight or balance even though great care has been taken to eliminate these. In fact, ordinary parlance has no unique common descriptor for the sensation elicited by I comparable to those for weight (light, heavy), sound energy (soft, loud), and others, even though the sensation is frequently encountered. Every time a body is moved in anything but translation, I makes itself felt as the resistance offered to having its rotational speed changed by the application of a torque.

Evaluations of the feel of a hand-held object commonly use the verbal descriptors heft and balance, which are reasonably analogous to M and CG for simple translational or static balancing motions of the object; the designer can thus translate likes and dislikes into appropriate changes. Experience in product design suggested that I might also contribute to dynamic feel, as when a golf club or tennis racquet is swung freely.

Both I and M are fundamental properties of a rigid body in the sense that Newton's second law requires knowledge of both for a complete determination of the body's translational and rotational motion; the force equals M multiplied by the translational acceleration, and the torque equals I multiplied by rotational acceleration. These relations reinforce the expectation that M and I are potential independent contributors to the feel of a manipulated object forced to undergo translational and rotational accelerations. Whereas human sensitivity to different weights has had a long and systematic investigation beginning with Fechner (3), we have found no published research on the analogous determination of sensitivity to different I 's. The functional significance of this sensitivity lies at least in its contribution to further classifying such elusive multidimensional constructs as the feel of a manipulated object important in its proper human factors design. Quantitating this sensitivity is also vital in designing further experiments to determine, for instance, the relative contributions of M and I to feel.

In classical psychophysical studies of human sensitivity to sensory stimuli, a value that can be distinguished from a reference 50 percent of the time is called the just noticeable difference (jnd). The ratio of the jnd to the reference is called Weber's fraction and is accepted as a measure of differential sensitivity to that stimulus in the region of the reference value such that small ratios indicate high sensitivity. For example, the Weber

Table 1. Physical properties of the cylindrical stimulus pieces. Seven pieces were constructed in each set between the minimum and maximum I with approximately equal separations. Experiments are designated by the lengths and outside diameters of the stimuli.

Set	Weight (g)	I_{\max} (g-cm ²)	I_{\min} (g-cm ²)	I_R (g-cm ²)
<i>Experiment 1: 12.7 cm by 1.91 cm</i>				
1	29.31 ± 0.61	793.55	76.71	391.93
2	39.32 ± 0.22	989.68	153.55	470.32
<i>Experiment 2: 68.58 cm by 3.18 cm</i>				
1	297.10 ± 1.81	441.91 × 10 ³	257.81 × 10 ³	347.95 × 10 ³
2	391.90 ± 1.36	610.06 × 10 ³	323.66 × 10 ³	462.63 × 10 ³
3	489.42 ± 2.27	779.79 × 10 ³	397.37 × 10 ³	580.51 × 10 ³

fraction for lifting weights of about 1/2 kg is approximately 1/50 to 1/30 (4).

In order to determine Weber's fraction for I , we used hollow cylindrical test pieces with two interior weights positioned to yield calculated values of I while maintaining the CG at the midpoint. Two experiments were conducted with test pieces whose lengths and weights were representative of metal safety razors (experiment 1) and tennis racquets (experiment 2) in order to place the sensations in the ranges of common experience. Table 1 lists the relevant measured physical properties of the test sets. The median value of each seven-piece set served as the reference for comparisons. The CG of all pieces was at the middle. Within each experiment, the pieces appeared identical. The I values were calculated about the point of grip; in experiment 1, the subject held the stimulus between the thumb and index finger on the CG ; in experiment 2, the subject used a full hand grip 7.62 cm from an end.

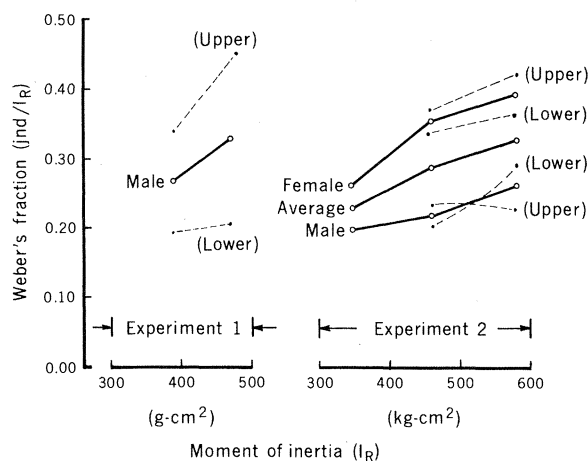
The method of constant stimuli (5) was used to determine sensitivity. The subject sequentially compared one of the pieces (including the reference) with the reference piece several times in the set and indicated which of the two felt more "top-heavy." Plotting the percentage of these judgments for each I value generated the usual ogival psychophysical

curve. The distance between the reference value (usually at 50 percent) and the 25 percent and 75 percent interpolated I values gave the lower and upper jnd, respectively. If no serious discrepancy existed between the two values, they were averaged to yield a single jnd.

Training was initiated with two transparent simulated test pieces showing the two slugs together in the middle (smallest I) or maximally separated (greatest I). Subjects examined and handled these pieces and were told that the piece with the slugs maximally separated was "more top-heavy" than the other. This essential training quickly produced proportions of judgments of "more top-heavy" highly correlated with I . Any other description could probably have been used if it were accompanied by the visual training. Subjects could distinguish differences but could not reliably determine which piece had more of the property in question without this training.

The small reference values of I (I_R) of experiment 1 produced upper jnd's and Weber fractions about twice that of the lower ones, whereas experiment 2 produced more nearly equal upper and lower values (Fig. 1). The jnd values in each case were interpolated from a single psychophysical curve fitted by least squares to the averaged responses of the subjects. Because the test pieces in the

Fig. 1. Differential sensitivity to moment of inertia (I) over two widely separated ranges of values. Small I corresponds to metal safety razors and large values are typical of tennis racquets. Horizontal scales differ between the two experiments. Both upper and lower Weber fractions are shown where they differ by more than 10 percent. Ten males were subjects in experiment 1. Ten different males and ten females were subjects in experiment 2.



two experiments had to be manipulated differently because their sizes and weights differed, aggregation of the two sets of results must be viewed cautiously. Humans are differentially sensitive to I , however, and the Weber fraction is about ten times that for lifted weights. If we use 0.28 as a representative value for Weber's fraction, we can interpret this sensitivity as follows. If a new pencil 19 cm long and twiddled about its center is compared with another of identical weight but 2.47 cm (13 percent) longer, the difference in sensation would be noticed about 50 percent of the time. In a weightless environment, if the two pencils were of the same mass density, the second pencil need only be elongated 1.63 cm (8.6 percent) overall. The formula $I = \frac{1}{12} ML^2$ (where L is length) approximates the moment of inertia about CG of a long thin cylindrical object such as a pencil. The female subjects were about 50 percent less sensitive than the males (Fig. 1), perhaps because they handle sports equipment less.

The M and I_R values of the test sets were monotonically related because of geometric constraints, so it is not certain whether sensitivity to I actually decreases with increasing I or M or some combination of both (6). For practical purposes, however, the Weber fractions given here are useful because it is difficult to construct similar objects with M and I values radically different from those of the test pieces. The Weber fractions are about the same in the two experiments even though the I and M values differ by 1000:1 and 10:1, respectively.

Quantifying human sensitivity to I is useful to those designing products, just as similar knowledge of weight perception is. At a more fundamental level, however, it is perplexing to encounter virtually no common recognition of the sensation in spite of frequent exposure to it; worse (from the designer's viewpoint) is erroneous verbal identification of it with weight or balance. These difficulties do not indicate that a person cannot perceive I , as these and other experiments (7) have established, nor do they signify that perception of I is unimportant. It is more likely that we do not interact with angular accelerations of a body as often as we do with translational ones (except perhaps in sports); we thus have infrequent need to make conscious torque comparisons and therefore never develop the necessary vocabulary.

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6. We have studied multidimensional scaling of weight and I varied in a 3 by 3 factorial design; naive subjects without training could perceive the simultaneous effects of each in making

paired comparison similarity judgments between test pieces although, as before, they could not describe the differences. In making these judgments, subjects appeared to weigh I much more than M , even though the test pieces were constructed a priori to have equal M and I interval sensitivities. This was accomplished by using jnd results from the experiments reported here for I and from the literature for M and spacing the stimuli on each dimension at approximately 1.45 jnd apart. The assumption in so doing was that the two stimuli would then be equally represented psychophysically.

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Effects of Frontal Eye Field and Superior Colliculus

Ablations on Eye Movements

Abstract. *Two parallel neural pathways are primarily responsible for the control of saccadic eye movements—one mediated through the frontal eye fields and the other through the superior colliculus. When both pathways are disrupted, control of saccadic eye movements is lost. Disruption of either pathway alone produces only subtle deficits.*

The majority of sensory and motor functions are under the control of more than one brain site. This well-known fact, coupled with the plastic properties of nervous tissue, accounts for the observation that when lesions are confined to single sites in the mammalian brain, often only limited or transient effects on sensory and motor functions are produced. The mechanisms involved in the control of saccadic eye movements are a good example. Even though considerable evidence indicates that in primates both the frontal eye fields and the superior colliculi are involved in the control of eye movements, bilateral ablation of either of these structures alone produces only relatively subtle or short-term deficits in oculomotor function (1-3).

Studies using single-cell recordings have shown that, in the upper layers of the monkey superior colliculus, cells respond selectively to visual stimuli; in the deeper layers, cells that discharge before saccadic eye movement predominate. Selectivity for the spatial location of visual stimuli as well as for the amplitude and direction of saccades is arranged in an orderly, topographic fashion (4). In the frontal eye fields, neurons sensitive to eye movement and to visual stimulation have also been found. The visual receptive fields are much larger than in the colliculus, and the topography is less well defined. The visual response of some of these cells is strongly enhanced when the monkey subsequently makes a saccade to that stimulus; eye-movement cells, however, seem to discharge only during and after saccades, not before them (5).

Electrical stimulation of both of these structures elicits saccades whose sizes and directions depend on the specific site of stimulation (6, 7). In addition, stimulation in the visual cortex also produces saccadic eye movements. Since both the frontal eye fields and the visual cortex project to the superior colliculus, the effects of electrical stimulation might be thought to be mediated through this structure. However, collicular ablation abolishes saccadic responses only for striate cortex stimulation; stimulation of the frontal eye field continues to produce eye movements at thresholds comparable to those found in intact animals (7). This suggests that in primates, visually triggered saccadic eye movements can be controlled through at least two channels: a visual cortex-superior colliculus-brainstem system and a frontal cortex-brainstem system. Past lesion studies may be interpreted to support this view in that ablation of either the frontal eye fields or the superior colliculus have produced only relatively limited deficits in gaze and in saccadic eye movements (1, 3).

The aim of our experiments was to determine what happens to visually triggered eye movements when both pathways are disrupted by the paired ablation of the frontal eye fields and the superior colliculi. We examined the effects of successive bilateral lesions in the frontal eye field and the superior colliculus in ten monkeys. The frontal eye fields were aspirated aseptically under visual control while animals were anesthetized. The superior colliculi were removed with radio-frequency lesions after the exact location