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 $I = {}^1/_{12}\, ML^2$ (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; naïve 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 radiofrequency lesions after the exact location

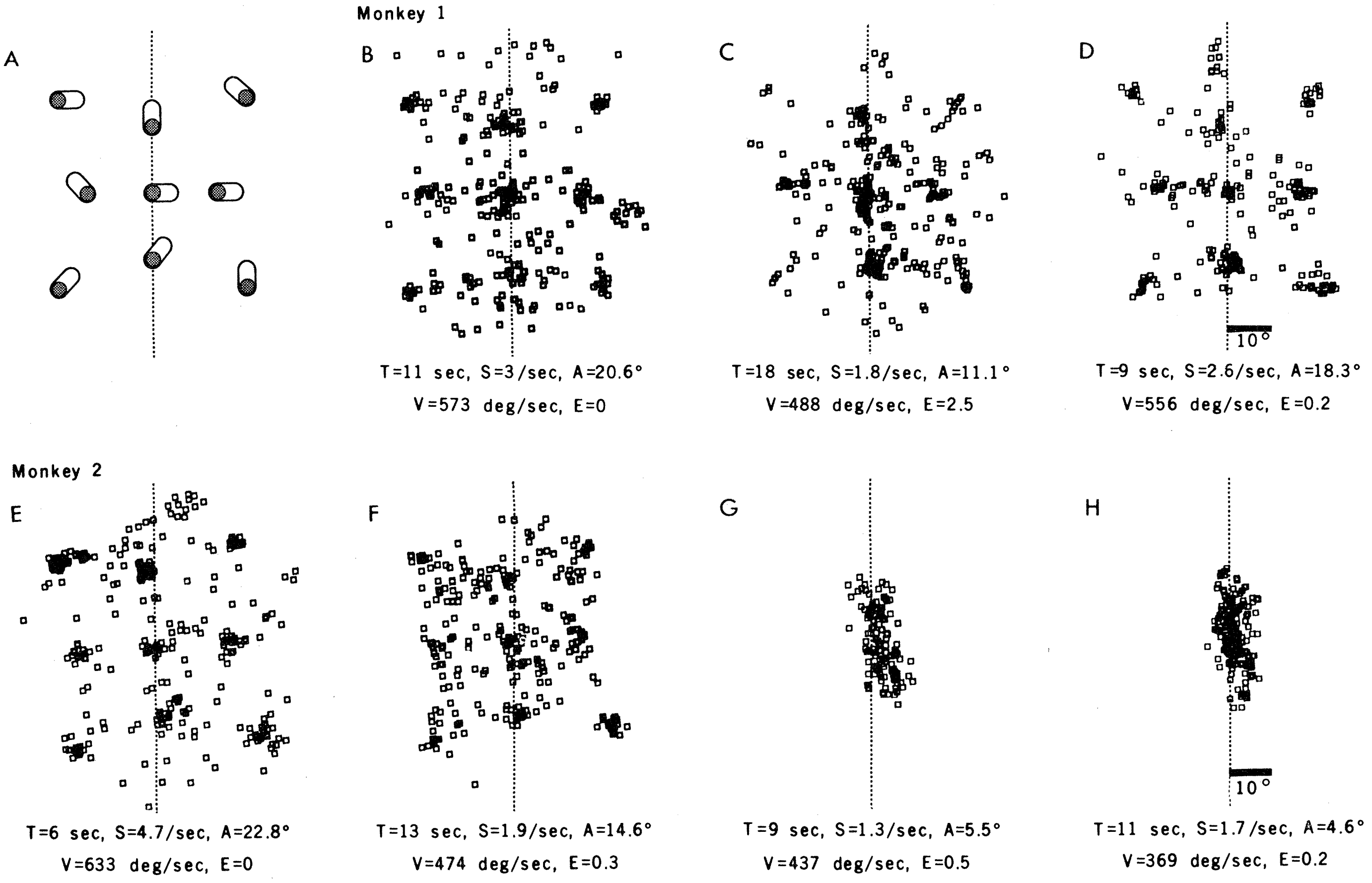

Fig. 1. Eye fixation patterns of two monkeys at various stages during the experiment. (A) Configuration of the apple board. (B) Fixation patterns of monkey 1 produced in the course of ten repeated preoperative trials. Data collected (C) 4 and (D) 24 days after bilateral ablation of the frontal eye field. Below each display are shown five measures computed for these data: mean time to complete task (*T*); mean number of saccades per second (*S*); mean saccade amplitude (*A*); mean saccade velocity (*V*); and mean number of errors (dropping of apple pieces or ignoring them) (*E*). In monkey 1, bilateral ablation of the frontal eye field produced temporary deficits on all measures, but, as shown in D, recovery was virtually complete. (E) Preoperative fixations by monkey 2. (F) Ablation of the superior colliculus caused deficits on all measures shown, but on day 4 the monkey could still fixate on targets. The additional ablation of the frontal eye field (G and H) produced a dramatic loss in targeting ability that failed to recover with time. (G) Targeting 57 days after the additional ablation; (H) after 134 days.

of this structure was determined with single-unit recordings (*3*). The two pairs of lesions were made 3 to 12 weeks apart, and the order was varied among animals. In six of the monkeys, a search coil had previously been implanted around one eye to enable us to record eye movements accurately (*8*), and in the others, electrooculographic electrodes were used. Skull screws were also implanted to allow us to immobilize the animals' heads during recording sessions.

Before lesioning, animals were trained to pick apple pieces out of a 34 by 34 by 1 cm Plexiglas "apple board" which had 9 or 17 randomly oriented 1.2 by 2.5 cm slits cut into it in various locations, each of which accepted a small piece of apple (Fig. 1A). The task was easy, yet necessitated careful hand-eye coordination. The animals had to orient their hands properly relative to the slit to successfully retrieve the desired apple piece.

A computer was programmed to detect saccades and fixations and to provide quantitative data for a number of eye-

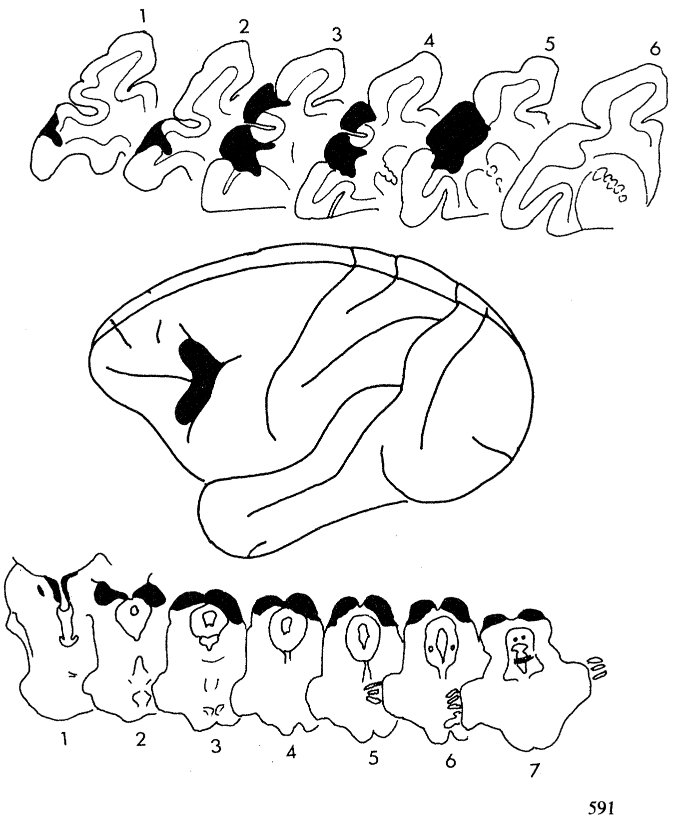

Fig. 2. Histological reconstruction of the lesions made in monkey 2. The large sketch is of the left hemisphere, with the shaded area showing the lesion of the frontal eye field. Serial coronal sections for this area appear above, shown 1440 μm apart. Section 6 is across the posterior bank of the arcuate; the lesion did not encroach into this region. The frontal eye field lesion in the right hemisphere, which is not shown, was similar but less extensive. The collicular lesions, shown for both colliculi, appear below with the left side of the brain to the left of each section. The coronal sections are 720 μm apart.

movement variables, including fixation locations, saccade sizes and directions, and velocities (*9*). Typically, fixations were analyzed for 8 to 20 repeated trials, each of which consisted of clearing the baited apple board. Fixation plots of normal monkeys showed a clustering of fixations at points where the apple pieces appeared on the board (Fig. 1, B and E). Both the 17-slot apple board and spontaneous eye movements yielded quite different clustering patterns.

In accordance with previous reports (*1, 3*), the effects of either frontal eye field or collicular lesions on visually guided saccadic eye movements were not dramatic. Ablation of the frontal eye fields produced a partial neglect; animals tended to leave some of the sites on the apple board unpicked and looked at peripheral targets less frequently. This effect was temporary; after 1 to 3 weeks, recovery was virtually complete, and fixation patterns and latencies became comparable to performance before the lesion was made (Fig. 1, B to D).

Superior colliculus ablation in otherwise intact monkeys produced several subtle deficits, which recovered little; the animals were able to make visually triggered saccades but accuracy decreased, as did the number, size and velocity of saccades (Fig. 1F).

In contrast, ablation of both the frontal eye fields and the superior colliculi produced a remarkably dramatic deficit: animals virtually ceased making organized saccades. They seemed to have lost the ability to target their eyes on visual stimuli. Monkey 1 was able to perform saccadic eye movements only within a limited range and showed low accuracy in targeting. This effect did not recover with time (Fig. 1H). We have kept animals for longer than 1 year without observing improvement. The extent and distribution of the remaining eye-movement activity varied among animals and appeared to be a function of spared tissue in the superior colliculus. In some animals the deficit was more pronounced than for monkey 2 (Fig. 1, E to H).

Figure 2 shows the histological reconstruction of the lesions for monkey 2. The collicular lesion in the right superior colliculus was more extensive than that in the left. Tissue sparing was especially evident on the left lateral margin of the superior colliculus (sections 3 and 4)—representing the lower right visual field near the vertical meridian—and near the midline (sections 5 and 6)—representing the upper vertical meridian. The residual eye-movement activity of monkey 2 appears to correspond to the tissue spared in the colliculi. Animals in which the superior colliculus was removed only partially or only superficially (leaving intermediate and deep layers intact) showed less pronounced deficits.

Although animals with the combined bilateral lesions could move their eyes only within a restricted range and targeted inaccurately, they attended to the entire visual field. Except for the period 1 to 3 weeks after the frontal eye field was ablated, they picked all or most of the apples on the board without directing their gaze correctly. When their heads were free, they oriented head and body toward items of interest.

We also examined several other kinds of oculomotor performance in these animals. Smooth pursuit and optokinetic nystagmus as elicited by moving objects and gratings showed a narrowed range corresponding to the deficit seen on the apple board task. The range of the vestibulo-ocular reflex, produced by rotating the monkey while the head was fixed, was also reduced immediately after surgery but recovered considerably over a period of several weeks or months. With the head free, eye movements induced by the vestibular system as compensation for a head movement were evident; however, such compensation was not typically preceded by saccadic targeting, as it is in intact animals.

These findings suggest that two pathways, one via the frontal eye fields and the other via the superior colliculi, are responsible for producing visual targeting by eye movement; when only one is damaged, the other can remain effective; when both are disrupted, organized saccadic eye movements are virtually abolished.

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Early Hominid Population Densities: New Estimates

Abstract. *Proportional faunal representations in excavated fossil occurrences (Shungura Formation, Omo, Ethiopia) are very similar to modern sub-Saharan mammalian faunal proportions in a variety of environments. Early hominids comprise between 0.6 and 1.6 percent of the excavated assemblage, corrected to reflect numbers of individuals. With allochthonous faunal localities for comparison, direct analogies to modern fauna suggest early hominid population densities of between 0.006 to 1.7 individuals per square kilometer. Calculations based on population densities of modern large mammals indicate that population densities of early hominids were between 0.001 and 2.48 individuals per square kilometer.*

In terrestrial biotopes, biomasses of herbivores, carnivores, and further links in the food chain are progressively smaller (*1*). Furthermore, among animals there is a tendency for herbivores to be more numerous, and for primary, secondary, and tertiary carnivores to be respectively less abundant (*1*). These ecological relationships can be used, in conjunction with faunal excavations, to reconstruct aspects of hominid Pliocene paleoecology.

The paleobiological significance of an excavated fauna depends on the particular agents responsible for its accumulation and the depositional environment in which it occurs; that is, its taphonomic history. Excavations in the lower Omo Basin, Ethiopia, considered here, have been reported (*2*). They occur in both high-energy depositional environments, such as point-bar and abandoned-channel deposits, and in relatively low-energy environments, such as backswamps and alluvial plain deposits.

Large accumulations of disarticulated and fragmentary bones, occurring in well-sorted and large grain-sized sediments, as in localities L.1 and L.398, (Table 1), are considered to represent al-