directly into pontine sites elicits cataplexy in cats (*18*) and that physostigmine elicits REM sleep in humans (*19*) and suggest that muscarinic cholinergic mechanisms are also involved in cataplexy. This cholinergic component may be involved in the decreased utilization of catecholamines and serotonin reported here.

Our results support a proposed theory linking the initiation and maintenance of REM sleep to reciprocal interactions and a critical balance between serotonergic, adrenergic, and cholinergic neuronal networks in the pontine area of the brainstem (*20, 21*). A final link in the medullary reticular formation would inhibit the discharge of extensor and flexor motoneurons via reticulospinal pathways (*22*). Our genetic studies of narcolepsy in Dobermans point to an autosomal recessive defect in a single gene (*4*). This gene may be involved in the regulation of biogenic amine metabolism or release—whether through enzymatic activity, receptor sensitivity, or uptake mechanisms.

While the results do not explain the basic defect in genetic narcolepsy, they do reflect an unequivocal deficit that will allow the formulation of testable neurochemical hypotheses. These findings are direct neurochemical evidence of a biogenic amine deficit in a genetic animal model of narcolepsy.

IVAN N. MEFFORD*
THEODORE L. BAKER
RICHARD BOEHME
ARTHUR S. FOUTZ
ROLAND D. CIARANELLO
JACK D. BARCHAS
WILLIAM C. DEMENT
Department of Psychiatry and Behavioral Sciences, Stanford University School of Medicine, Stanford, California 94305

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* Present address: Department of Chemistry, Boston College, Chestnut Hill, Mass. 02167.

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Path-Guided Apparent Motion

Abstract. *A curved gray path, briefly flashed between two alternately displayed black dots, induced a compelling illusion of a single dot moving back and forth over that path. The minimum interval between dot onsets yielding this apparent motion increased not with the direct distance between the dots but, linearly, with the length of the curved path.*

In the classical phenomenon of apparent motion, two stationary visual stimuli presented in alternation and in different spatial locations (Fig. 1A) yield the illusion of a single object moving back and forth over the shortest path between them (*1, 2*). This phenomenon provides evidence for the internalization of principles of object conservation and least action (*3–5*). The brain evidently prefers the interpretation that a persisting object moved over the most direct path consistent with the available evidence rather than an interpretation that the object moved over some longer path or, worse, that one object went out of existence and a second object simultaneously materialized at another location. Moreover, the preferred interpretation tends to be automatically instantiated in the most concrete perceptual form, as an actual movement over the interpolated path. Indeed, apparent motion can be indistinguishable from real motion if the two locations are sufficiently close together (*6*).

Although apparent motion is also possible over larger spatial separations, it then tends to be less compellingly real. Furthermore, the brain's ability to achieve a concrete instantiation of motion over a longer path seems to be constrained by inherent limitations on its own rate of processing. Thus, in accordance with Korte's third law (*2*), the maintenance of good apparent motion requires, with each increase in the spatial separation between the stimuli, a corresponding increase in the delay between the onset of one stimulus and the onset of the other [called the stimulus onset asynchrony (SOA)]. Indeed, the minimum SOA yielding good apparent motion increases linearly with this distance (*5, 7, 8*). If the SOA is shorter than specified by this law, the appearance of a single stimulus moving back and forth breaks down into the appearance of two stimuli blinking on and off independently.

Discrimination between real and apparent motion is presumably based on whether or not sensory receptors along the retinal path corresponding to the experienced motion are physically stimulated. We conjectured that the brain interprets such intermediate sensory events as the "blurred streak of motion" over the path even when those intermediate events occur so rapidly that their temporal order is not resolved. This conjecture led to our exploration of two specific hypotheses.

The first is that the brief presentation of a faint stationary connecting band between two alternately presented stimuli (Fig. 1B) should stimulate the relevant intermediate receptors and, despite the absence of temporal sequencing along the path, provide a good imitation of the blur of rapid motion. In support of this hypothesis, when we flashed a low-contrast homogeneous gray band of this sort during the brief interval between two black dots, our observers reported that the illusion of motion of the dot became more compelling. Although too brief to be seen for what it was, the band seemed to provide the previously missing blur of the dot's transit. However, a determination of the exact conditions under which such "path-guided" apparent motion is indiscriminable from real motion must await equipment more suited to the parametric control of real motion.

The second hypothesis, which is the primary focus of this report, includes two claims about this apparent motion itself: (i) By briefly flashing a curved band between the two alternately presented dots (Fig. 1C), we should be able to induce the illusion of movement over that curved path. (ii) The minimum SOA for good apparent motion over that curved path should then depend on the length of the path and not, as in the original formulation of Korte's law, on the direct distance between the two dots.

In striking confirmation of this second hypothesis, when we independently varied length of path (Fig. 1D) and direct distance (Fig. 1E), the critical SOA did not increase with the direct distance but did increase, remarkably linearly, with the length of the presented path (Fig. 2A). We take this as significant new evidence for our claim, already supported by other kinds of evidence (*4, 8, 9*), that during apparent motion the brain carries out an analog simulation of an actual motion over a particular trajectory in space (*3, 5*).

Moreover, not only were observers able to experience the motion over the variously curved paths (Fig. 1, D and E), but with appropriately adjusted timing, they were even able to experience the motion around a completely closed circle (Fig. 1F). In accordance with the already posited principles of object conservation and least action, the brain presumably favors the interpretation that one object made a rapid circular excursion rather than the interpretation that a compact, solid object momentarily vanished and was briefly replaced by an extended, faint ringlike object. To our knowledge, this is the first report of the apparent motion of a stimulus into itself.

We presented the black dots and light gray paths (Color Aid paper No. 1A) against a white background by illuminating different fields of a four-field tachistoscope in a repeating sequence. In width, each circular dot and uniform gray path subtended a visual angle of 0.42°. The interdot field, which contained the gray path, lasted only 5 msec—a duration that in preliminary explorations yielded near optimum apparent motion for the degree of contrast and range of lengths of our paths. Observers were asked to keep their eyes fixed at the center of the region defined by the presented path and to try to see the dot as moving back and forth over the path. For each stimulus configuration, the observer then repeatedly pressed a key, which increased the duration of both dots in 10 percent steps from an initial duration of 100 msec each, until the desired motion was first experienced.

In a variable path-length condition, the distance between the dots was always 3° in visual angle, but the length of the connecting path varied, from trial to trial, between the straight path of 3° and four circularly curved paths with arc lengths of 4°, 6°, 9°, and 12° of visual angle (Fig. 1D). In a fixed path-length condition, the length of path was held

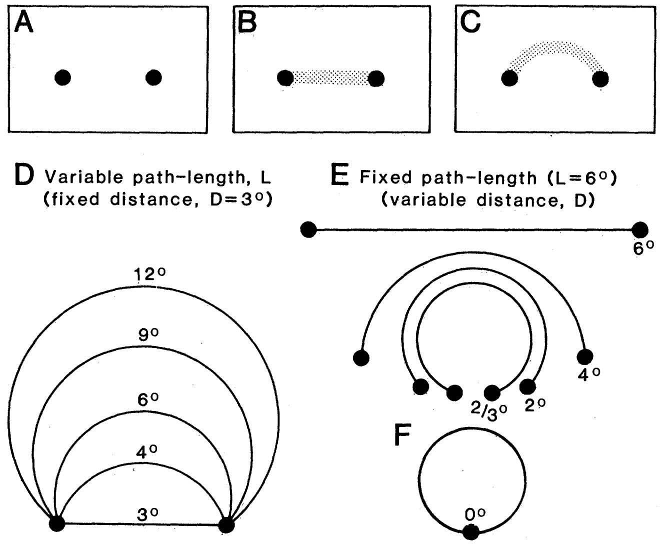

Fig. 1. Stimulus configurations for (A) classical and (B and C) path-guided apparent motion and schematic illustrations of the paths presented in (D) the variable path-length condition and in (E and F) the fixed path-length condition. The attached numbers give visual angles corresponding to the lengths of the paths (D) or distances between the dots (E and F). [The presented paths were uniformly gray, not stippled as shown here (B and C).]

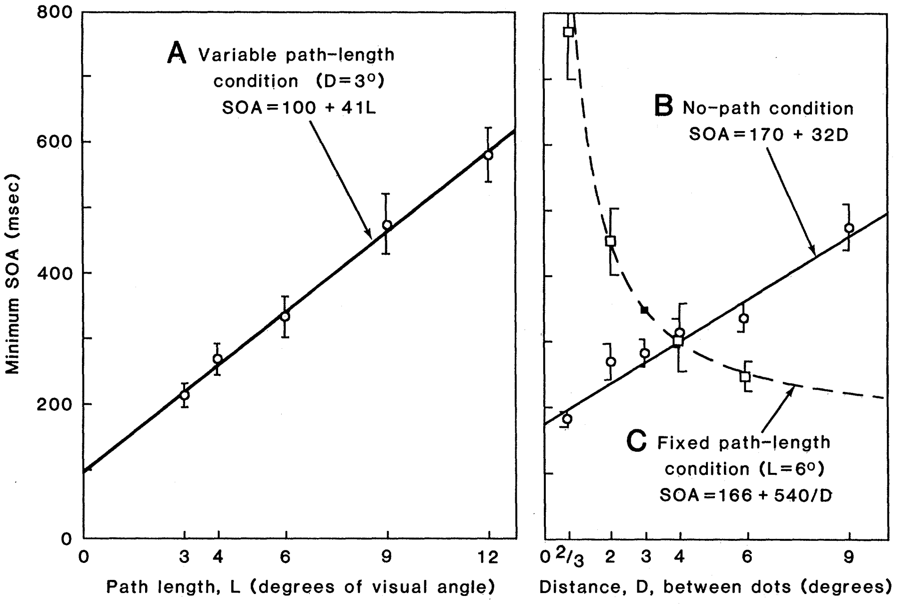

Fig. 2. Minimum stimulus onset asynchrony (SOA) for good apparent motion. (A) Over a presented path, as a function of the length of that path in the variable path-length condition; (B) between the two dots, as a function of their direct distance of separation in the absence of a presented path; and (C) over a presented path, as a function of the distance between the dots in the fixed path-length condition. Each point gives the median of the ten observers' mean critical SOA's for the specified length (*L*) or distance (*D*), and each vertical bar gives an approximation to ± 1 standard error of the median, based on the quartile deviation of the ten observers' means in place of the standard deviation. (Means and standard deviations could not be computed for $D = 0$ and $D = 2/3$ in the fixed path-length condition, because the one observer generally requiring the longest SOA's was unable to experience motion over these closed or nearly closed circles.)

constant at 6° of visual angle, but the path was adjusted in curvature so that the direct distance between the two terminal dots varied, from trial to trial, between 6°, 4°, 2°, 2/3°, and 0° of visual angle (Fig. 1, E and F). Finally, in a no-path condition, the 5-msec interstimulus field was blank (Fig. 1A), and the dots were separated by 2/3°, 2°, 3°, 4°, 6°, or 9° of visual angle. In this control condition, observers increased the SOA until they achieved, simply, "good apparent motion." This was usually experienced along the straight path between the dots. The session for each condition consisted of five practice trials followed by a random sequence of recorded trials yielding, for each of ten observers, four trials for each spatial configuration used in that condition (*10*).

When the path formed a nearly complete circle, observers reported that the illusion of motion over the path was more difficult to achieve and, when achieved, less compelling. Below the critical SOA, the dot appeared to jump directly across the gap in the circle rather than moving around the curved path (*11*). When the path formed a complete circle (Fig. 1F), the 5-msec interstimulus interval proved to be too short for the eye to register the disappearance of the dot and, hence, no motion was experienced. However, the illusion of motion (either clockwise or counterclockwise) around the complete circle was achieved by nine of the ten observers when we then inserted a 200-msec blank white field both before and after the 5-msec circular path.

When the two dots were fixed 3° apart, the minimum SOA for the emergence of apparent motion over the presented path increased linearly with the length of that path (Fig. 2A); a similar linear trend emerged for each of the ten individual observers.

The standard test for departure from linearity seemed inadvisable because fluctuations in critical SOA, rather than being independent of SOA, were roughly proportional to it. Accordingly, linearity was assessed in two other ways: (i) by robust regression, which is relatively insensitive to such heteroscedasticity, and (ii) by performing the standard test for linearity only after subtracting, from each observer's SOA's, the intercept of the linear function for that observer (as estimated in the robust regression) and then logarithmically transforming the resulting dependent and independent variables in order to nullify heteroscedasticity (*12*). The coefficients for robust linear fits varied considerably between observers, but the intercepts averaged about 100 msec, and the slopes (which were positive for all ten observers) averaged about 41 msec per added degree of visual angle of path length (Fig. 2A). There was, moreover, no evidence that the residual departures from linearity were more often positive or negative for any of the five lengths of path [$\chi^2(5) = 2.46$]. Finally, the test for departures from linearity after logarithmic transformation yielded F ratios (with 4 and 15 degrees of freedom) that were not significant ($\alpha = .05$) for nine of the ten observers (*13*).

The group results for the two comparison conditions are again representative of the data for individual observers. The linear increase in critical SOA with distance between the dots when no path was presented (Fig. 2B) is in accord with Korte's third law. However, the higher intercept and larger deviations here than in Fig. 2A may reflect the weaker character of the experienced motion in the absence of a presented path.

When the two dots, while still varying in distance of separation, were connected by a path of fixed 6° length, the critical SOA (now for motion over that path) no longer increased with distance between the dots. Instead, this SOA decreased inversely with that distance, as if approaching an asymptotic value for large separations (Fig. 2C). We fitted the curvilinear function to these data by adjusting one parameter after constraining the (broken) curve to pass through the point, indicated by the small black square in Fig. 2C, for which $D = 3°$, $L = 6°$, and the critical SOA, as determined by the fitted line in Fig. 2A, is 346 msec. The goodness of fit thus attests to the close agreement between the results for the variable and fixed path-length conditions (*10*). The sharp increase in the critical SOA as the two dots were brought close together is, we believe, a consequence of the competitive pull of the alternative short-circuit motion directly across the gap in the nearly completed circular path (*11*).

When the dots were made completely coincident (Fig. 1F), the median critical SOA for motion around the full circle became 648 msec. However, the special circumstances of this case (including the required addition of 400 msec of blank interstimulus interval) make close comparisons with the other critical SOA's problematic.

We suggest that path-guided apparent motion may offer a practical technique for displaying more realistic and tightly controlled motions despite limitations on the rate at which successive images can be generated, as in low-cost computer graphics, band-limited telecommunications, or motion-picture animation.

ROGER N. SHEPARD
SUSAN L. ZARE

*Department of Psychology,
Stanford University, Building 420,
Stanford, California 94305*

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10. The first eight of the observers were administered the three conditions in three separate sessions in the order mentioned, and the last two observers, who were less familiar with classical apparent motion, started instead with the no-path condition. (However, the results did not vary noticeably with the amount of previous experience or order of conditions.) Two other potential observers reported difficulty in experiencing good apparent motion and did not complete the experiment.
11. Farrell and Shepard (*4*) reported an analogous phenomenon arising in apparent rotation of two-dimensional objects.
12. The statistical analyses were carried out by L. Maloney. The method of robust regression was drawn from the statistical package S furnished by Bell Telephone Laboratories, Murray Hill, N.J. 07974. This method iterates to convergence through the use of a Huber weighting function for individual points and then adds two iterations with a Bisquare weighting function. The test for linearity of the logarithmically transformed data was that described by S. Weisberg [*Applied Regression Analysis* (Wiley, New York, 1980), p. 83].
13. The value of F ranged between 0.3 and 2.9 for these nine observers, but reached 10.8 for the remaining observer, whose unexplained departure from linearity consisted entirely of exceptionally low critical SOA's for the straight 3° path.

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