Other factors, including mechanical disturbance, defense against predators, and overcrowding, may also cause colonies to change nests (*12*). Finally, even our overfed laboratory colonies eventually emigrated. When we examined the contents of the abandoned bivouac, we found large amounts of uneaten booty in various stages of decomposition. It is thus possible that chemical products of booty decay may also promote emigrations. Nevertheless, it seems clear that food scarcity is a principal cause of emigrations in *N. nigrescens*. And, given recent evidence that changes in the alimentary condition of ant larvae can produce corresponding changes in the level of adult arousal (*13*), the link between food abundance and brood excitation seems equally clear-cut for army ants.

Longitudinal field studies on *N. nigrescens* by Schneirla and Mirenda (*14*) show that the emigration frequency of nomadic colonies ranges between 74 and 88 percent. Because this corresponds best to the behavior of our underfed laboratory colonies, we are led to the conclusion that nomadic raids rarely bring in enough booty to satiate the larval broods. According to Mirenda's study (*7*), this situation is exacerbated by the very occurrence of emigrations, which take valuable time away from foraging. Perhaps the key to understanding the relationship between foraging and emigrations in *N. nigrescens* is Wilson's (*15*) principle of stringency—that time-energy budgets evolve to fit periods of greatest ecological stringency. The large number of species of *Neivamyrmex* in tropical America suggest a neotropical origin for this genus. Given the intense competition among army ant species, selection favored colonies that frequently shifted foraging areas. When food is abundant and competition reduced, as it is in southeastern Arizona, colonies are unable to suspend emigrations because of constraints imposed by the mechanisms suited to more severe conditions.

HOWARD TOPOFF
JOHN MIRENDA*
Animal Behavior-Biopsychology Program, Hunter College of City University of New York, New York 10021, and *American Museum of Natural History, New York 10024*

References and Notes

1. T. C. Schneirla, *Proc. Am. Philos. Soc.* **101**, 106 (1957).
2. E. O. Wilson, *The Insect Societies* (Harvard Univ. Press, Cambridge, 1971), pp. 55-72.
3. T. C. Schneirla, *Army Ants: A Study in Social Organization* (Freeman, San Francisco, 1971), pp. 149-168.
4. C. W. Rettenmeyer, *Univ. Kans. Sci. Bull.* **44**, 281 (1963).
5. T. C. Schneirla and A. Y. Reyes, *Anim. Behav.* **17**, 87 (1969).
6. All colonies were culled to contain approximately 6000 adults and 4000 larvae. One-half gram of booty represents approximately one-fourth of the mean amount captured by a nomadic colony of this size, as determined by Mirenda (*7*).
7. J. Mirenda, thesis, City University of New York (1978).
8. Booty consisted of termites and pupae of ant species belonging to the genera *Formica, Camponotus, Acanthomyops, Pheidole*, and *Trachymyrmex*.
9. The arrangement of the nests and runways was dictated by an additional study (in preparation) on the relation between booty location and emigration direction.
10. That these results are not an artifact of the laboratory is shown by Mirenda's field study (*7*), in which artificially fed nomadic colonies did not emigrate for up to five consecutive days.
11. U. Maschwitz and M. Mühlenberg, *Oecologia (Berlin)* **20**, 65 (1975).
12. B. Hölldobler, *Behav. Ecol. Sociobiol.* **1**, 3 (1976); A. Peacock *et al., Misc. Publ. Dep. Agric. Scotl.* **17**, 1 (1950); N. Weber, *Bol. Entomol. Venez.* **6**, 143 (1947); E. O. Wilson, *Behav. Ecol. Sociobiol.* **1**, 63 (1976).
13. M. V. Brian, *Physiol. Comp. Oecol.* **4**, 329 (1957); ———, *Insect Soc.* **9**, 295 (1962); ——— and J. Hibble, *ibid.* **10**, 71 (1963).
14. T. C. Schneirla, *Insect Soc.* **5**, 215 (1958); Mirenda's (*7*) very thorough study included eight nomadic phases from six colonies of *N. nigrescens*.
15. E. O. Wilson, *Sociobiology: The New Synthesis* (Harvard Univ. Press, Cambridge, 1975), p. 142.
16. The study was conducted at the Southwestern Research Station of the American Museum of Natural History, and was supported by grant 76-17366 from the National Science Foundation.

* Present address: Department of Entomology, Texas A & M University, College Station 77843.

26 September 1979; revised 6 December 1979

Do the Two Eyes Constitute Separate Visual Channels?

Abstract. *A two-interval forced-choice procedure was used to study monocular detection of a briefly presented low-contrast sine-wave grating pattern. Uncertainty about which eye was stimulated degraded detection performance for stereoblind observers but not for normal ones. These results relate to selective monocular suppression, stereopsis, and other forms of binocular interaction and suggest the level at which inputs to the two eyes are combined neurally.*

Some question has always existed about the extent to which the two monocular images are separately processed, in terms of their spatial content, before being combined binocularly. This question bears directly on issues relating to binocular interaction, such as stereopsis, suppression, and single vision. According to one school of thought, a more or less complete analysis of monocular form precedes stereopsis and fusion. This hypothesis, which asserts that the two eyes constitute separate visual channels, was championed early by Sherrington (*1*) and has been expressed in more contemporary writings as well (*2*). Alternatively there is the viewpoint that information from the two eyes is integrated earlier in visual processing, prior to stages involving more refined analysis such as pattern recognition. Julesz (*3*) is a proponent of this view, and there are those who believe that cortical neurophysiology provides support for this single channel position (*4*). We have attempted to evaluate these two alternatives with a detection uncertainty paradigm.

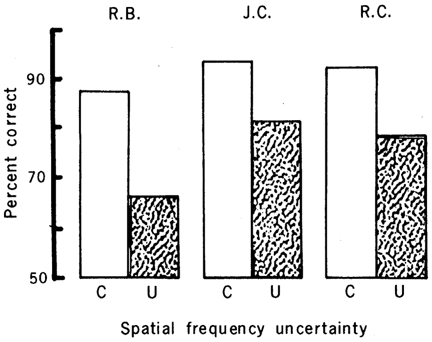

Fig. 1. Detection on a two-interval forced-choice procedure of a sinusoidal grating presented binocularly under conditions of spatial frequency certainty (*C*) and uncertainty (*U*) for three observers. Each score is based on 200 trials and represents combined data for 1 cycle/deg and 4 cycle/deg. For each observer, values for 1 and 4 cycle/deg differed by less than 5 percentage points. Before each block of trials, observers were exposed to the stimuli used for that block at easily observable contrast, thus ensuring that for the certainty conditions the observer knew the properties of the stimulus.

Our experiments capitalized on the fact that uncertainty about the spatial or temporal characteristics of a stimulus can degrade detection. This effect has been demonstrated on a variety of tasks in both audition (*5*) and vision (*6*). An example of the effects of uncertainty is illustrated by Fig. 1. These values were obtained in a two-interval forced-choice experiment; the observer's task was to indicate in which of two successive 1-second intervals (each defined by a tone) a vertical, sinusoidal grating pattern was presented. The grating was generated electronically on a cathode-ray tube (CRT) and presented binocularly. Details of the apparatus are given elsewhere (*7*). Observers viewed one of two 5° by 7° CRT displays separately with each eye. The vertical sinusoidal grating pattern which served as the stimulus was presented on both CRT's and had a total duration of 350 msec. At first, blocks of 100 trials were carried out under the certainty condition: Throughout the block of trials the observer knew the spatial frequency of the test grating as we determined the contrast value that yielded some arbitrary percentage correct (*8*). We repeated this maneuver for gratings of 1 and 4 cycle/deg, in both instances with complete certainty about spatial frequency. Next, using these same contrast values, we redetermined performance over a block of 200 trials in which the two spatial frequencies (100 trials each) were randomly intermixed (the uncertainty condition). Performance over this block of trials dropped by an average of 15 percent, thus confirming the potent effects of uncertainty. After the uncertainty conditions, we repeated blocks of trials under certainty conditions. Performance on these trials equaled that of the earlier certainty trials. In other experiments we have found that the magnitude of this drop in performance is inversely related to the difference in spatial frequency between the two test gratings. Moreover, we have found comparable losses in detectability by introducing uncertainty concerning the area of the retina receiving the pattern or uncertainty about grating orientation. In general, it seems that the potency of uncertainty depends on the extent to which the detection task requires the monitoring of several sensory channels simultaneously (*9*).

Suppose we establish for each eye separately a contrast level yielding, say, 75 percent correct detection under conditions of the observer's always knowing which eye is to receive a grating pattern as well as being certain about its spatial frequency. Next we use this pair of contrast values to measure detection performance with the observer unable to predict the eye receiving the grating from trial to trial (*10*). If the two eyes operate as separate channels, we would expect this uncertainty about eye of origin to degrade performance. For observers with normal stereopsis, however, uncertainty about eye of origin had no influence on grating detectability (Fig. 2A), which indicates that the two eyes behave as a single channel.

We have repeated this experiment with three observers who show no stereopsis; for two of these stereoblind observers, eye uncertainty did degrade detection performance (Fig. 2B) by an amount comparable to that produced by spatial frequency uncertainty in normal observers. For a third stereoblind person, eye uncertainty had little, if any, effect (*11*). The decrement in performance shown by two of the stereoblind observers did not arise from monocular suppression, since detection errors were distributed equally between the two eyes.

Stereoblind observers, in contrast to normal observers, exhibit reduced interocular transfer and binocular summation (*12*), but are capable of utrocular (eye-of-origin) discrimination (*13*). One explanation for these differences is that normal and stereoblind observers have different proportions of monocular and binocular cortical neurons. It seems reasonable to attribute the differential effects of eye uncertainty in normal and stereoblind observers to these same putative dissimilarities in the degree of cortical binocularity. According to this hypothesis, people with good stereopsis have a normal array of binocular neurons, which blend together inputs from the two eyes early in visual processing, even before the level of simple detection. On the other hand, an unusually high proportion of monocularly innervated neurons in persons with poor stereopsis means that information from the two eyes remains sufficiently segregated at least to the level of detection to introduce a channel uncertainty effect (*14*). By analogy to the neurophysiological effects of early visual deprivation, the extent to which the two eyes constitute a single visual channel may depend on the degree to which the eyes work in a coordinated, balanced fashion during the so-called critical period.

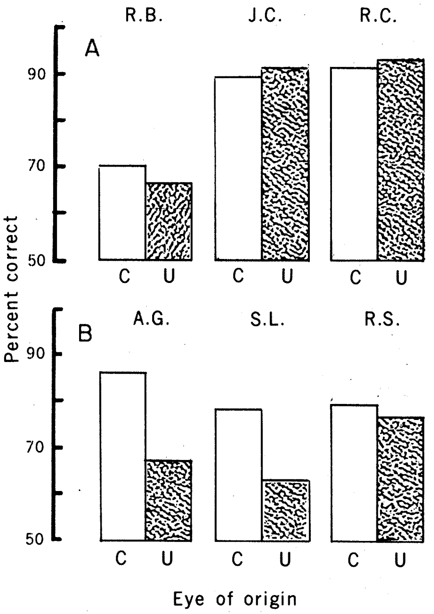

Fig. 2. Detection of a sinusoidal grating under conditions of certainty (*C*) and uncertainty (*U*) regarding eye of origin. Each score is based on 200 trials and represents combined data for right and left eyes. For the certainty condition, values for the right and left eyes differed by less than 5 percentage points. Before each block of trials, observers were exposed to stimulation of the eye or eyes to be used for that block at easily seen contrast levels, thus ensuring that for the certainty condition the observer knew which eye was to be stimulated. (A) Data for observers with normal stereopsis, tested at 1 cycle/deg. (B) Data for stereoblind observers. Observer R.S. was tested at 4 cycle/deg. Others tested at 1 cycle/deg.

Some stereoblind observers in our experiments have occasionally reported a degree of voluntary control over which eye they use. Presumably this control would involve suppression of the unused eye, as is seen in alternating strabismus. The eye-of-origin uncertainty effects shown by our stereoblind observers lend some support to their subjective accounts. The fact that uncertainty affected performance on a forced-choice task renders it unlikely that apparent suppression of one eye represents a criterion shift rather than decreased sensitivity.

The eye-of-origin uncertainty paradigm developed for this experiment has considerable potential as a psychophysical tool for isolating monocular from binocular neural channels.

ROBERT H. CORMACK
Department of Psychology, New Mexico Institute of Mining and Technology, Socorro 87801

RANDOLPH BLAKE
Department of Psychology, Cresap Neuroscience Laboratory, Northwestern University, Evanston, Illinois 60201

References and Notes

1. C. Sherrington, *The Intergrative Action of the Nervous System* (Yale Univ. Press, New Haven, Conn., 1906).
2. K. Ogle, *Researches in Binocular Vision* (Hafner, New York, 1964).
3. B. Julesz, *Foundations of Cyclopean Perception* (Univ. of Chicago Press, Chicago, 1971).
4. P. O. Bishop, in *Handbook of Sensory Physiology*, R. Jung, Ed. (Springer-Verlag, New York, 1973), vol. 7.
5. J. A. Swets and S. T. Sewell, *J. Acoust. Soc. Am.* **33**, 1586 (1961); W. Larkin and G. A. Greenberg, *Percept. Psychophys.* **8**, 179 (1970).
6. T. Cohn and D. J. Lasley, *J. Opt. Soc. Am.* **64**, 1715 (1974); D. S. Greenhouse and T. Cohn, *ibid.* **68**, 266 (1978); N. Graham, J. Robson, J. Nachmias, *Vision Res.* **18**, 815 (1978); R. Sekuler and K. Ball, *Science* **198**, 60 (1977).
7. R. Blake and R. H. Cormack, *Percept. Psychophys.* **26**, 53 (1979). The displays were presented in a mirror stereoscope at a viewing distance of 110 cm and were viewed through natural pupils with the observer's head securely positioned by a dental impression board. Electronic and digital circuitry [C. Enroth-Cugell and T. Robson, *J. Physiol. (London)* **187**, 517 (1966)] was used to generate on the matched-CRT's grating patterns of sinusoidal luminance. Average luminance remained constant at 7.1 cd/m^2, obviating the need for artificial pupils. A shaped rise-fall gate introduced and withdrew the grating pattern gradually with a 50-msec time constant. The clear borders of the displays provided compelling fusion stimuli. The cover-uncover test was used to achieve accurate binocular alignment of the displays and minimize fixation disparity. To ensure that the gratings were in precisely the same rela-

tive locations on the two CRT screens, their relative phases were adjusted until an observer with good stereopsis reported that the fused pattern appeared in the plane of the CRT face.

8. Observers adapted to the light of the observing chamber for at least 5 minutes before each session. Observers were instructed to keep both eyes open and to fixate the center of the screen throughout all trials. They initiated their own trials by depressing a pushbutton and indicated whether a grating pattern appeared during the first or second 1-second interval by throwing a lever switch left or right, respectively. Correct responses produced a feedback tone to the observer. Before each block of trials, observers were allowed to trigger a number (10 to 12) of trials with the grating pattern set at high (10 percent) contrast to familiarize themselves with the stimulus to be detected. Rest periods could be taken at any time and were followed by a readaptation period.
9. D. Green, *Signal Detection and Recognition by Human Observers*, J. A. Swets, Ed. (Wiley, New York, 1964).
10. The same apparatus and procedure were used for this experiment. The grating pattern was displayed on only one of the two CRT's. For the certainty conditions, the same eye was stimulated throughout a block of 100 trials; for the uncertainty condition, the eye stimulated was randomly varied from trial to trial. For each observer the same spatial frequency was used throughout the experiment. Again, observers triggered a number of familiarization trials at high contrast before each block of trials. After the uncertainty condition, the certainty condition was repeated. Performance always returned to the earlier certainty levels.
11. All observers were tested for stereopsis with a modified Howard-Dolman device, the modified Ortho-Rater, and random-element stereograms (*3*). The three stereoblind observers have other visual characteristics: R.S. displays a convergent strabismus of approximately 10°, with corrected acuities of 20/22 [oculus dexter (O.D.)] and 20/40 [oculus sinister (O.S.)]; S.L. displays a 6.33° esophoria, has no history of manifest strabismus, and has corrected acuities of 20/18 (O.D.) and 20/17 (O.S.); A.G. is a former esotrope who was surgically corrected at the age of 4, with follow-up surgery at the age of 11, is currently orthophoric but mildly ambliopic with acuities of 20/20 (O.D.) and 20/30 (O.S.). Observers with refractive corrections wore them during testing.
12. S. Lema and R. Blake, *Vision Res.* **17**, 691 (1977).
13. R. Blake and R. H. Cormack, *Science* **203**, 274 (1979). Normal observers were tested at 1 cycle/deg, a spatial frequency at which R.B. and J.C. can make eye-of-origin discriminations reliably. The absence of an uncertainty effect for these observers suggests the possibility that successful eye-of-origin discrimination at low spatial frequencies by normal observers is mediated by a mechanism different from that used by stereoblind observers.
14. D. Westendorf, A. Langston, D. Chambers, and C. Allegretti [*Percept. Psychophys.* **24**, 209 (1978)] reported stereoblind binocular detection performance to be near that expected from probability summation, as if the eyes were independent detectors. These results complement those of the present study.
15. Supported by NIH grant EY01596 and NSF grant BNS 7817948. R.B. holds NIH career development award EY00106.

24 September 1979; revised 10 December 1979

On the Status of *Australopithecus afarensis*

In this comment it is our purpose to establish the relationship between *Meganthropus africanus* Weinert 1950 and Johanson's replacement name for this taxon, as well as to discuss the errors that we believe to have been incorporated by Johanson and White (*1*) into their taxonomic speculations.

The first publication making the name *Australopithecus afarensis* available was apparently a report of a meeting sponsored by the Swedish Academy of Sciences (*2*). Since this is an unusual and potentially hazardous means of announcing a new zoological name, it must be asked if the name proposed in this publication satisfies the International Code of Zoological Nomenclature (*3*) in terms of availability. Reference to the Code indicates that it does. Ideally the description of a new taxon should be accompanied by a differential diagnosis; however, this is not required by the Code. The statement in (*2*) that "This taxon is characterised by definite bipedalism, marked sexual dimorphism (larger males, smaller females) but no brain expansion" satisfies the criterion of the purported differentiation of a taxon. The correct author citation of the new name is: *Australopithecus afarensis* Johanson, 1978 since the authorship of a new taxon goes to its proposer and not to the person reporting its announcement (Article 50a).

Johanson indicated in the original description, as reported by Hinrichsen (*2*), that the type-series used as the basis of his new name consisted of the Pliocene hominids from Hadar and Laetoli; however, no type-specimen was designated. Although the fact that the original publication did not include the designation of a type-specimen affects neither the availability nor the potential validity of the new name, the issue of the type-specimen of *A. afarensis* does present other problems that must be clarified. In cases such as this where a type-specimen was not designated in the original publication, Article 74a (i) provides that a subsequent worker may designate a lectotype from the type-series. The first reviewers of this taxon to designate a type-specimen were the proposer of the name and two other workers (*4*). Although the date of publication of this review is incompletely specified [Article 21b (ii)], it is certain that it was published substantially later than the original publication, since one of us (M.D.L.) withdrew her name from the review as late as August 1978. In the review (*4*), the Laetoli hominid (L.H. 4) mandibular specimen was, therefore, erroneously designated as the holotype rather than the lectotype, since a holotype can only be designated in the original publication of a new taxon.

The review by Johanson *et al.* (*4*) also introduces a number of other far more serious problems into the already unnecessarily confused realm of hominid taxonomy. In addition to designating a lectotype under the term holotype, they give a list of the specimens of the type-series under the inappropriate heading of paratypes (this should be paralectotypes according to Recommendation 74E of the Code) in which they include the Garusi maxillary fragment collected by Kohl-Larsen in 1939 (*5*). This important specimen from the Laetoli locality in Tanzania is the holotype of *Meganthropus africanus* Weinert, 1950 (*6*). Their inclusion of the Garusi 1 specimen in the type-series of *A. afarensis* and their listing of *M. africanus* as a synonym of this name has the effect of making *A. afarensis* a replacement name (junior subjective synonym) for Weinert's *M. africanus*. Johanson was correct in giving a new name to Weinert's species because his inclusion of this species in the genus *Australopithecus* Dart, 1925 (*7*) meant that the nominal species *Australopithecus africanus* (Weinert, 1950) had to be rejected since it was now a junior secondary homonym of *Australopithecus africanus* Dart, 1925 (Article 53). This article of the Code is essential because it precludes the absurdity of two species within the same genus bearing the same specific name.

As used by Johanson *et al.* (*4*), the name *A. afarensis* clearly does not identify a new species. Rather, it only enlarges the hypodigm of Weinert's species *M. africanus* and provides a necessary replacement name to apply to this species when it is included within the genus *Australopithecus*. The name *afarensis* is valid as a substitute for Weinert's prior name only (i) when Weinert's holotype and the L.H. 4 lectotype are included in the same species and (ii) when this species is classified in a genus in which Weinert's name is a junior homonym. If ever this species is considered to be generically distinct from the taxon represented by Dart's holotype of *A. africanus*, then the valid specific name must revert to *africanus* Weinert if it is the senior available name within the recognized species-group (Article 59c). In this latter case, Johanson's name becomes an invalid junior synonym. This procedure complies with the rules set out in the Code (Articles 59b and 60b) requiring that all junior homonyms be rejected and replaced and that a junior secondary homonym be restored as the valid name of a taxon whenever a zoologist believes that the two species-group taxa in question are not congeneric (Article 59b).

In Johanson and White's article on the