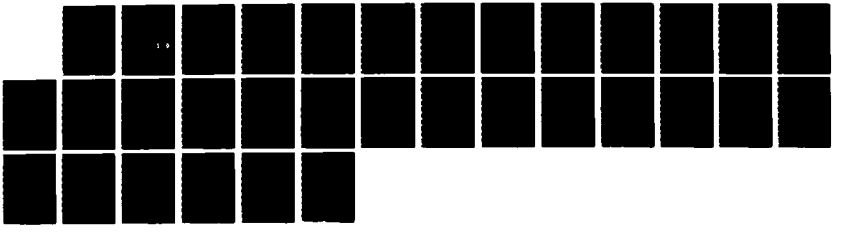
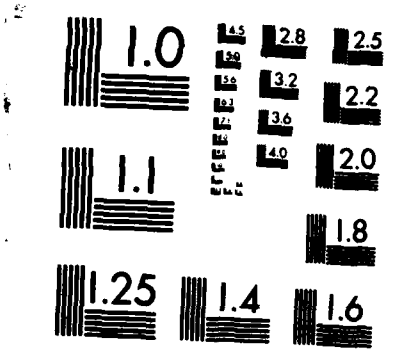
AD-A174 062 CORTICAL PLASTICITY AS REVEALED BY OCULAR DOMINANCE SHIFT: EFFECTS OF LIMITED VISUAL ENVIRONMENTS(U) BROWN UNIV PROVIDENCE RI J D DANIELS ET AL 03 NOV 86 TR-33 1/1

UNCLASSIFIED N00014-86-K-0041 F/G 6/16 NL





SECURITY CLASSIFICATION OF THIS PAGE (When Data Entered)

REPORT DOCUMENTATION PAGE

READ INSTRUCTIONS BEFORE COMPLETING FORM

1. REPORT NUMBER: #33
2. GOVT ACCESSION NO.:
3. RECIPIENT'S CATALOG NUMBER:

4. TITLE (and Subtitle): Cortical Plasticity as Revealed by Ocular Dominance Shift: Effects of Limited Visual Environments

5. TYPE OF REPORT & PERIOD COVERED: TECHNICAL REPORT

6. PERFORMING ORG. REPORT NUMBER:

AUTHOR(s): J. D. Daniels and Diane J. Kraus

8. CONTRACT OR GRANT NUMBER(s): N00014-86-K-0041

PERFORMING ORGANIZATION NAME AND ADDRESS
Center for Neural Science Division of Engr.
Brown University
Providence, Rhode Island 02912

10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS: N-201-484

CONTROLLING OFFICE NAME AND ADDRESS
Personnel and Training Research Program
Office of Naval Research, Code 442PT
Arlington, Virginia 22217

12. REPORT DATE: November 3, 1986

13. NUMBER OF PAGES: 28 pages

MONITORING AGENCY NAME & ADDRESS (if different from Controlling Office):

15. SECURITY CLASS. (of this report):

15a. DECLASSIFICATION/DOWNGRADING SCHEDULE:

16. DISTRIBUTION STATEMENT (of this Report)
Approved for public release; distribution unlimited. Publication in part or in whole is permitted for any purpose of the United States Government.

17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)

18. SUPPLEMENTARY NOTES
To be published in Behavorial Brain Research.

19. KEY WORDS (Continue on reverse side if necessary and identify by block number)
Visual Cortex
Development
Single Units
Ocular Dominance shift
Social Isolation

20. ABSTRACT (Continue on reverse side if necessary and identify by block number)
Kittens were dark-reared until about 51/2 weeks of age, at which time each kitten was allowed one week of 12 hr/day monocular experience in a controlled visual environment. In most cases mean luminance of the sawdust in the conditioning cage was in the range 0.3 to 15 mFL. In half the cases a large mobile rotated outside the cage, and spotlights were directed to illuminate the mobile. At the end of the conditioning week, we recorded from cells in area 17, noting ocular dominance and other receptive field properties for each cell. Kittens which had their monocular experience alone had virtually no ocular dominance shift.

DD FORM 1 JAN 73 1473 EDITION OF 1 NOV 65 IS OBSOLETE
S/N 0102-LF-014-6601

SECURITY CLASSIFICATION OF THIS PAGE (When Data Entered)

If kittens were accompanied by a sibling, or a toy, or got to view their mother at a 50 cm distance, they had partial OD shifts. If the illumination were raised into the photopic realm, then socially isolated kittens also showed a partial shift.

We think that the presence of the mother allows a kitten to have a greater experience of optic flow and reduces separation anxiety; these two factors are probably important for an environment in which developmental plasticity can occur in visual cortex.

Cortical Plasticity as Revealed by Ocular Dominance Shift: Effects of Limited Visual Environments

J.D. Daniels & Diane J. Kraus

Division of Engineering & Center for Neural Sciences, Box D,
Brown University, Providence, RI 02912

Technical Memo to ONR.

key words: visual cortex, development, single units, ocular dominance shift, social isolation.

Acknowledgements: Supported by ONR contract N00014-86-K-0041. Flaxedil was kindly supplied by Davis & Geck. Eva Pressman was especially helpful in the early stages of these experiments, both with conceptual ideas and data gathering. We thank Martha Motuz, Mitchell Sutter, Kathleen Cullen, Sharon Lubkin, Heidi Horstmann, Mark Kroe, Chris Parry and Alan Saul for additional help collecting the data. The main set of experiments were performed 1983-1985. Ford Ebner provided expert advice concerning histological location of 17/18 borders. Martha Motuz drew Fig. 1 and Donald Kraus, Jr. helped with the computer graphic displays for Fig.'s 2-10.

July, 1986

Abstract

Kittens were dark-reared until about 5 ½ weeks of age, at which time each kitten was allowed one week of 12 hr/day monocular experience in a controlled visual environment. In most cases mean luminance of the sawdust in the conditioning cage was in the range 0.3 to 15 mFL. In half the cases a large mobile rotated outside the cage, and spotlights were directed to illuminate the mobile. At the end of the conditioning week, we recorded from cells in area 17, noting ocular dominance and other receptive field properties for each cell. Kittens which had their monocular experience alone had virtually no ocular dominance shift. Kittens which had their monocular experience with their mothers had a complete ocular dominance shift. If kittens were accompanied by a sibling, or a toy, or got to view their mother at a 50 cm distance, they had partial OD shifts. If the illumination were raised into the photopic realm, then socially isolated kittens also showed a partial shift.

We think that the presence of the mother allows a kitten to have a greater experience of optic flow and reduces separation anxiety; these two factors are probably important for an environment in which developmental plasticity can occur in visual cortex.

1. Introduction

A kitten's visual perception depends upon the physiological condition of its optical & CNS pathways (internal factors) and upon objects visible in its nearby world (external factors). The external factors are the reflectance properties of non-luminous objects in the kitten's environment, the placement of sources to illuminate those objects, and the position of the kitten with respect to both the objects and the sources (see Frisby, 1979, chpt.'s 6 & 7; Marr, 1982, chpt. 3, for general discussion). We are concerned with how the relationships among this triad of external factors influence the development of the neurons in the kitten's visual cortex. In particular we want to know how external arrangements affect developmental plasticity revealed by a week of monocular deprivation (MD)--after which a kitten in a normal visual environment has nearly all of its area 17 neurons driven exclusively by the opened eye (Wiesel & Hubel, 1963; Olson & Freeman, 1975). In one way a concern about external visual relationships has an ecological optics theme (Gibson, 1979) but in another way it links our findings about external arrangements with internal, pharmacological, factors, such as the presence or absence of catecholamines in visual cortex (Bear & Daniels, 1983).

In two previous studies (Daniels *et al.*, 1984; Daniels & Saul, 1986) we examined parameters of illumination as they affected our index of developmental plasticity--ocular dominance (OD) shift of area 17 neurons after a week's worth of MD. We found that dim, flickering light, especially in the range 2-10 Hz, substantially prevented the expected OD shift, while steady illumination, in a scotopic[1] range, was adequate for promoting a complete OD shift. Cynader *et al.* (1973) and Olson & Pettigrew (1974) raised *binocularly-viewing* kittens in 0.5 Hz strobe light and recorded diminished orientation & direction selectivity, although ocular dominance seemed near-normal. In our strobe study of MD kittens (Daniels & Saul, 1986) we also saw, at 2 & 4 Hz rates, neurons which failed to show orientation & direction selectivity but which, as a population, did achieve a partial ocular dominance shift.

In the present study we change the emphasis from illumination to object illuminated. We wanted to know whether near or far objects, moving or stationary, two-dimensional or three-dimensional, *in a dim but steadily lit environment,* mattered for the ocular dominance plasticity of the kitten's visual system. As will be seen from the results, it appears that a kitten requires the presence of nearby, three-dimensional objects, whether moving or not, to promote an OD shift. An especially effective "visual stimulus" is a kitten's mother, and in fact our results suggest that without its mother present a kitten may suffer enough separation anxiety to reduce the effectiveness of otherwise visible objects.

Others researchers have limited what a kitten can view, then searched in visual cortex for changes in single unit receptive field properties. Pettigrew & Freeman (1973) raised kittens in a planetarium environment. The kittens were restricted to viewing point sources of light and as a consequence developed receptive fields which preferred *smaller-than-normal* stimuli. Furthermore the cells in planetarium-reared kittens failed to develop direction-selectivity, perhaps because, like strobe-reared kittens, nothing moved in their visual world. Using a array of small, green, blinking LED's instead of point sources in a black canopy, we (Daniels & Garrett, unpub. obs. & Garrett, 1981) confirmed Pettigrew & Freeman's (1973) findings, and also

[1] *Scotopic* is a human psychophysical term, but it is likely the levels of illumination we used were not enough to drive the cone system in the cat retina (Mouat, 1985). Ramoa *et al* (1985) have shown that receptive field properties of *adult* cat visual cortex area 17 neurons remain relatively unchanged over a wide range of luminance levels, except that at low levels of illumination OFF responses are less vigorous

showed that if kittens were monocularly deprived in such an environment, no ocular dominance shift occurred. Van Sluyters & Blakemore (1973) conditioned kittens in cylinders whose walls were painted with small spots and recorded similar, but less dramatic, preferences of cells for small stimuli in otherwise normally-sized receptive fields. Hirsch & Spinelli (1971) and later Stryker *et al.* (1978), utilizing special goggles which permitted kittens to view only vertical or only horizontal stripes, showed that, as a population, cells in area 17 came to prefer the orientation of the conditioning stripes. With goggles fitted over the eyes, each eye viewed a pattern uncorrelated with the other eye's pattern, and as a consequence few *binocular* cells were encountered. The resulting ocular dominance histogram was U-shaped, like that from kittens with strabismus (Hubel & Wiesel, 1965).

Simply conditioning kittens in cylinders with vertical or horizontal stripes on the walls was not nearly as effective as the goggle technique (Stryker & Sherk, 1976). However, Berman & Daw (1977) and Daw *et al.*, (1978) found that a kitten which looked at vertical stripes on a drum *rotating* around it would develop area 17 preferences for the *direction of movement* of the drum. Further, viewing such a rotating drum with only one eye could cause an ocular dominance shift to the opened eye. Their results, when compared with those from viewing of *stationary* stripes, suggest that image movement can be an important influence on ocular dominance plasticity. Actually, Daw *et al.*, (1978) found an OD shift after *reversal* of a previous lid closure, a result similar to Rauschecker & Singer (1981) who reversed the conditioning orientation and the viewing eye, around six weeks of age, and found that the only cells which reshifted OD preference were those which also preferred the new conditioning orientation.

Clearly it is possible to arrange limited visual environments which bias or disrupt the normal development of area 17 cells' receptive fields. To what extent such disruption can be monitored by restriction to monocular viewing, then recording ocular dominance in area 17, is one of the questions addressed in this paper.

2. Methods

Animals. We recorded from 30 kittens born in our quarantined colony. For each kitten, the data base, Table I, shows the conditioning environment, and the ocular dominance (OD) index. Each litter stayed in the normally lit home colony until about two weeks of age, at which time the litter was transferred to a light-tight darkroom.

Lid Closure. All kittens except for the 3 dark-reared ones received left lid closure. We anesthetized each kitten with 25 mg/kg ketamine, i.m., plus 3 mg/kg ace-promazine, i.m. We then sutured the left nictitating membrane to the inner lid margins with 8 stitches of 5-0 Mersilene (braided polyester). We did *not* cut lid margins. After suturing, we sealed the opposing lid margins with cyanacrylate. Each time before a kitten was moved from the darkroom to the conditioning chamber, we inspected the lid closure. If the lids had parted but the nictitating membrane was still pulled up, we reglued the outer lid margins without additional anesthesia. This lid closure technique produced less inflammation and less incidence of infection than the usual method of cutting and suturing the lid margins.

Environmental Conditions. Connected by a doorway to the darkroom is the conditioning room. Figure 1 indicates the possible arrangement of animals, light sources and other visible objects in the conditioning room. The room's walls, ceiling and floor were painted ultra-flat black. On a 75 cm pedestal, we placed a cage (80 x 70 x 50 cm high). The cage was constructed of black columns 5 cm thick, which supported black chicken wire. The roof of the cage was a hinged lid which could frame an opaque sheet or a translucent diffuser. (See footnote to Table I for cases which used the roof occluder or diffuser.) In the ceiling above the cage, we installed a track lighting system which held four incandescent spotlights each of whose direction of illumination could be adjusted. We

could control the voltage delivered to the spotlights with a variable transformer (Variac) on the AC line.[2] A timer limited duration of illumination to 12 hours per conditioning session.

The spotlights could illuminate a mobile suspended at either 150 or 75 cm from the center of the cage. The mobile elements were pastel cloth shapes which could be made to rotate gently (approximately 25 rev/min) by a fan under the cage. The individual components of the mobile had relatively constant reflectances, regardless of orientation, because of their Lambertian surfaces.

In two cases (C359, C361; Table 1) we suspended a toy animal into the cage. The toy, which resembled a mother cat in size, color and texture, was hung from the cage roof by elastic strap.

Photometry. Unless the translucent diffuser was in place, the inside of the cage provided little visual stimulation other than sawdust, and the black-painted food and water bowls. We used the sawdust as a standard from which to determine luminance. See the third column of Table I. Luminance was measured with a Photo Research low level photometer. To determine the dimmest levels of luminance, we extrapolated down from source current measurements, and used the 4th power black body radiation law (Halliday & Resnick, 1981). At places in the paper we refer to "scotopic", "mesopic" and "photopic" light levels. We realize these are terms generally designated for human psychophysics (Riggs, 1971; Boynton, 1966), but we found them useful shorthand descriptions. In our "scotopic" lighting, colors were not distinguishable to the human caretakers, whereas in our "photopic" they clearly were.

Table I, under *conditioning environment*, groups the nine conditions under which kittens had monocular experience:

1. scotopic isolation with mobile
2. absolute darkness with littermates
3. photopic isolation without mobile
4. mesopic isolation without mobile
5. scotopic with mother and mobile
6. mesopic with mother and without mobile
7. scotopic with stuffed animal and mobile
8. very dim illumination with mother and without mobile
9. scotopic with mother held at 50 cm distance from kitten

Except for the dark-reared, each kitten received at least seven days of monocular experience, 12 hours per day, spending the other 12 hours in the dark with mother and siblings. If a kitten were to be isolated from its mother during conditioning, then 6 hours after the start of a session the kitten would be reunited with its mother, in the dark, for a half hour.

Surgical Preparation. Single-unit recording from visual cortex began with a tracheotomy and femoral vein cannulation performed under ketamine-promazine anesthesia (25 mg/kg and 3 mg/kg, i.m., respectively). After a scalp incision, bilateral craniotomies exposed both areas 17. We tore the overlying dura with electrolytically-sharpened tungsten picks. (See Bear & Daniels, 1983, and Nelson *et al.*, 1985, for other details of surgical preparation.) We paralyzed with an initial dose of 20 mg Flaxedil i.v., when we placed the kitten on a stereotaxic frame. The rails of the frame, angled 14° downward, allow the animal's area centralae to project straight ahead onto a tangent screen 114 cm distant. We maintained paralysis with 12 mg/kg/hr Flaxedil in 5% dextrose-saline infused at 3 ml/hr, along with the administration of a gas mixture consisting of 75% N_2O, 23% O_2, and 2% CO_2. Long-term anesthesia was maintained by 75% N_2O. Occasionally, doses of 2 mg Nembutal i.v. were given if the kitten showed synchronized EEG activity to a sharp paw pinch. In addition to EEG activity, we monitored rectal temperature, heart rate, and end-tidal CO_2. We kept CO_2 at 3-4% by tuning the CO_2 level in the gas mixture, or the stroke volume.

After we dilated the pupils with atropine, we inserted contact lenses with 4 mm artificial pupils, selected to give zero or slight positive correction. With an ophthalmascope, we determined the positions of the optic discs, then used Olson & Freeman's (1980b) data to infer the area centralae positions on the tangent screen.

[2] In two cases (F332, M344, Table I) illumination was provided by a small fluorescent tube set for its maximum output of 70 mFL

Single Unit Recording. Two Levick (1970) microelectrodes, 6 mm apart, were lowered into the areas 17. The electrodes were moved down by a 2 ½ micron resolution stepping motor system. Electrode signals were amplified by electrometer op amps (Analog Devices 515), and filtered. After multiplexing, the selected signal could pass through antilog amplifiers (Analog Devices 759 N & P), which have more gain for larger inputs. The filtered and amplified signal provided input to a window discriminator, whose output was sent to time-stamping memory buffer and thence to a software-based histogrammer (MINC 11/23).

Cell Classification. After isolating a unit, we plotted the receptive field (RF) of the dominant eye, noting RF position and size, location of ON and OFF regions, and preference for stimulus shape, direction and speed. We labeled a cell *aspecific, immature,* or *selective,* depending on the sharpness of its orientation tuning. Finally, we classified the ocular dominance of the cell according to Hubel and Wiesel's (1962) seven category scheme. After finishing with a cell, we either switched to listen to the other hemisphere's electrode, or we advanced both electrodes 100 μ, and searched for a new recording site.

Sometimes an electrode would settle at a site which provided only spontaneous activity, or silence. We would tr for 15 minutes to evoke a reliable visual response, using hand-held cards, strobe, images on the tangent screen, or a magician's wand. If nothing reliable could be found the site would be declared Unclassifiable and we would move on. Before an unresponsive site was entered in the data base, we determined that the electrode was not in white matter (see histology, below). Number of unresponsive sites are listed for each animal in a column of Table I.

We sometimes encountered cells in area 18; they were distinguished physiologically by better responses to fast-moving ($>$ 16°/sec) stimuli and larger RF size (Orban *et al.*, 1980), and anatomically by the criteria given below.

Histology and the 17/18 Border. Recording proceeded for about 30 hours; at the depth of the last unit we lesioned both hemispheres with 10μA current through each electrode for 20 seconds. We sacrificed the kitten with an overdose of potassium tartrate *i.v.* After perfusion with saline and formaldehyde, a 4 cm x 4 cm x 2 cm thick brain section was blocked out in the plane of the electrodes and was floated in 30% sucrose/10% formalin. We sectioned the tissue coronally every 40 microns using a Hacker cryostat, and Nissl stained those sections to reveal the electrode track. Microscopic search for the cytoarchitectural criteria of Tusa, *et al.*, (1978), helped us find the 17/18 border. Once we identified the border we noted whether either of the electrode tracks crossed it. If a track crossed into area 18, we noted the depth and went back to the cells recorded in that track to label those from area 18.

In this study we are concerned only with area 17 cells. For each animal we tabulated results from all the area 17 cells into an *ocular dominance (OD) histogram* and calculated an ocular dominance index. In this paper, the OD histograms of groups of animals are shown in the figures listed in the right-most column of Table I.

3. Results

Kittens with monocular experience in social isolation.

Even with what would seem to be a moderate amount of steady visual experience, distributed over a week, a monocularly deprived kitten may show virtually no ocular dominance shift of area 17 neurons, if the experience takes place in social isolation and if the overall illumination for the experience is dim (scotopic).[3]

Consider the first group of 9 kittens listed in Table I, each of whom had monocular experience (ME) with a mobile hung 75 or 150 cm away from the kitten's conditioning cage. Fig. 2, an ocular dominance (OD) histogram of the 362 classifiable units recorded in these kittens, shows only a slight shift toward the open right eye. The second-to-last column of Table I has the computation of "shift index" for each of the kittens--for Fig. 2 the average is 0.41. This number can be obtained directly from Fig. 2 by adding together the percentages of units in the

[3] By "steady" we mean that the illumination source did not flicker at all during the 12 hours each day the kitten was in the conditioning room, by "scotopic" we mean that the luminance of the sawdust in the conditioning cage was less than 10 milli foot Lamberts (mfL)

two groups of cells most dominated by the open eye. As can be gleaned from Table I, the OD shifts expected from the first group of nine failed to occur regardless of whether (1) the mobile rotated from the breeze of a hidden fan or was held rigidly motionless; (2) the mobile was moved 75 cm closer to the conditioning cage (which increased its apparent area by a factor of 4 and its luminance by a factor of two); (3) the normally opaque roof of the cage was replaced by the translucent diffuser, allowing more light into the cage interior.

The quality of responses from the socially isolated, mobile-viewing kittens was different from the quality of responses we recorded from 3 dark-reared kittens. A calculation from the "units" part of Table I indicates that, for the dark-reared kittens, 25% of the recording sites were non-visual, whereas only 3% of the mobile-viewing kittens' recording sites were non-visual. Both the dark-reared and mobile-viewing kittens had about 15% "selective"[4] responses. The ocular dominance histogram of the visually responsive units from the dark-reared group is Fig. 3; there is no OD shift.[5]

If the mobile is removed and the illumination increased to a brighter (photopic) range, then, as the third group of MD kittens in Table I shows, a substantial, but not complete, ocular dominance shift will result. Fig. 4 is the composite OD histogram for three such kittens; the average shift index is 0.72, whereas 1.00 would represent a complete shift.

We know from the next group of three isolated kittens, whose composite OD histogram is shown in Fig. 5, that if we lower the illumination to a moderate (mesopic) level, then much less OD shift occurs. The average shift index for this group was 0.45. Kittens in the Fig. 5 group, as in the "photopic" group, did not view the mobile.

Kittens conditioned with their mothers.

Two of the conditions for socially isolated kittens, those represented by Fig.'s 2 and 5, were repeated with the mother of the kitten present. Fig. 6 is the composite OD histogram for five kittens allowed to view the mobile in dim light, accompanied by their mothers. Fig. 6 can be compared directly to Fig. 2; a much greater shift is evident with the mother present--the average shift index is 0.83, vs 0.40 for Fig. 2. One kitten of the Fig. 6 group had its ME with a sibling instead of its mother, and another (C358) died after only ten units were studied. The next group of three MD kittens, represented by the histogram of Fig. 7, were in moderate (mesopic) illumination with their mothers. No mobile was present. Here we recorded the most complete OD shifts of the study--average 0.96 by our index. The conditions of the Fig. 7 group can be compared directly with the socially isolated conditions of Fig. 5, where the shift index was only 0.46, less than half of Fig. 7's value.

The mother acts as a visual stimulus for the kitten's near environment, and as a stress reducer. The next experiments were designed to test the importance of these two factors for promoting ocular dominance shift. Two MD kittens dealt with a cloth-covered toy animal suspended by elastic thread from the cage roof. Their combined OD histogram is Fig. 8, which shows a partial shift, but one greater than what we saw for isolated kittens who had only an out-of-cage mobile to look at. One kitten had a week of monocular experience, with its

[4]Selective means that there was a least one direction of stimulus movement for which the cell gave no response at all--see Methods for more details

[5]Both dark-reared and mobile-viewing kittens were placed in the dark around two weeks of age, so the only difference in visual experi-

mother, in very dim ("starlight"--0.01 mfL) illumination. This kitten had no OD shift (Fig. 9) but unlike dark-reared kittens, it had no unresponsive recording sites. Another kitten was able monocularly to see its mother, who was in a second chicken-wire cage 75 cm away, but not able to interact with it. This kitten's OD histogram is Fig. 10, which shows a partial shift--one greater than the typical shift for a mobile at the 75 cm distance. Thus simply being able to see its mother is important for promoting ocular dominance shift, but physical interaction seems necessary for a complete shift, at least at the levels of illumination we used.

Other findings.

Age. Inspection of Table I suggests that, at least over the range of 23 days to 54 days, age is not an important factor in determining whether or not social isolation affects ocular dominance shift. Most of our kittens were weaned during the seventh week of life, so some of our data are from weaned, and some from un-weaned kittens.

Selectivity. Because all the kittens went into the darkroom around the second week of life, the orientation and direction selectivities of units would be less developed at the start of ME than if the kittens had had normal experience up to that time. However, we did not document much improvement in selectivity in those kittens, especially the ones conditioned with their mothers, compared to the shifts in ocular dominance we saw. The average of selective cells from all the socially isolated kittens (represented by Fig.'s 2 & 5) was 16%, while the corresponding percentage for those conditioned with their mothers (represented by Fig.'s 6 & 7) was 20%. Perhaps our strict criteria for selectivity[6] or the average age of the conditioned kittens being greater than 6 weeks accounted for this lack of change in selectivity compared to ocular dominance.

Area 18. Examining OD classifications of 107 cells considered by RF field properties and histological location to be in area 18, we found no evidence to contradict the general findings for ocular dominance shift and selectivity changes of area 17 cells; however we had too few cells/animal to generate statistically significant results.

4. Discussion

Histograms of area 17 neurons from monocularly deprived (MD) kittens, who were allowed one week of visual experience in social isolation, did not show any shift toward the opened eye (see figures 2 & 5). This lack of shift was in spite of the kittens' environment being steadily lit, and objects (including a three-dimensional mobile) being continuously visible. On the other hand, for several MD litter-mates of the socially isolated kittens, environmental conditions were unchanged except for the accompaniment of each kitten *by its mother;* in these kittens area 17 ocular dominance (OD) shift was virtually complete (see figures 6 & 7).

Level of illumination.

That isolated MD kittens had no OD shift depended somewhat on the luminance being in

ence between the two groups was the one week of isolated mobile-viewing just before recording

[6]A unit was required to have no evoked response to at least one of twelve directions tested in order to qualify as selective. If it had a small response in some directions, and a bias for a larger responses in other directions, then we classed it as "immature". Normally reared kittens from our colony have 80% or more selective responses by our criteria

the scotopic or mesopic[7] realm. Some of our results here (see Fig. 4) and in Daniels & Saul (1986) suggest that increasing the level of illumination may be of help in allowing an isolated MD kitten to shift OD. As general illumination increases into the photopic realm, acuity improves, response latency decreases and color discrimination appears. In humans, these effects can be explained, to an extent, by differences between rods and cones and their central actions. In cats, rods outnumber cones 10:1 in the area centralis and 100:1 otherwise (Steinberg et al., 1973). In spite of this, the great majority of cells beyond photoreceptors in the cat visual system are influenced by both rods and the 555nm cones (Hammond & James, 1971; Kolb & Famiglietti, 1974; Mouat, 1985). Ramoa *et al.*, (1985) have recently studied receptive field properties of cat area 17 neurons in conditions of decreased illumination. They found that OFF responses were much more diminished than ON, but orientation and spatial frequency tuning were relatively unaffected.

If illumination is *flickering*, then even if a kitten is with its mother, OD shift may not occur (Daniels *et al.*, 1984; Daniels & Saul, 1986). For example, if the mobile[15] is replaced by a television screen tuned to a broadcast, the flickering, dim light is insufficient to promote an ocular dominance shift. If 16 Hz strobe is used, however, a complete shift occurs.

In their study of ocular dominance shift of kittens who viewed a rotating striped drum, Berman & Daw (1977) apparently isolated the kittens from their mothers, but used bright photopic illumination of the stimulus. The OD shifts they obtained are, from the point of view of this study, evidence that increased illumination can compensate for the stress of isolation from the mother, in promoting a shift.

With regard to the present results, perhaps the somewhat increased responsiveness of units during conditions of greater stimulus contrast (Bisti et al., 1977; Sanseverino et al, 1979; Ramoa et al., 1985) aids the mechanisms of ocular dominance shift. One possibility is that a greater postsynaptic response causes a more rapid synaptic modification, as modeled, for example, in Cooper (1985). Cooper's model predicts that units which shift ocular dominance have developed orientation selectivity beforehand. Because we dark-reared our kittens before allowing them a limited visual experience, we had a chance to test the prediction, since a dark-reared kitten loses selectivity while retaining binocularity. In this paper we report only on binocularity changes, since even in the most shifted cases we still recorded from many cells which were specific in their orientation preferences. As Daw et al. (1978) reported, the periods of susceptibility for ocular dominance and direction selectivity are not identical, with direction selectivity being largely determined by the end of a kitten's sixth week of life.

Whereabouts of the mother cat.

What is it about the presence of a MD kitten's mother that promotes a greater ocular dominance shift? We know that some, but not all, of the shift can be achieved by substituting a cloth animal, or a sibling, for the mother (see Fig. 8). Clearly the mother provides an effective visual stimulus in the immediate vicinity of the kitten. The fan-driven mobile, even at its closer positioning, was in no case (see Table I) responsible for an OD shift index greater than 0.54. Furthermore, in one pilot recording from a MD kitten (#455) whose mother was visible, but at a minimum of 50 cm (the closest approach of the mobile), we found a partial

[7]To repeat an earlier qualification, "scotopic", "mesopic" and "photopic" are properly terms from human psychophysics, their use here

shift, with an index of 0.64.

These results suggest that the experience of optic flow--of being able to approach and visually explore nearby objects--may be important in the proper development of the kitten's visual system. On the other hand, movement of stimulus alone may be less important. An experiment to test these notions is offered at the end of Discussion.

The mother's physical presence is likely also to reduce *separation anxiety* in her kittens (Reite & Field, 1985). The quality of separation anxiety is age- and species-dependent (Rosenblatt & Siegel, 1981), with most research having been done on rodents and primates. Separation anxiety can be contrasted with isolation stress: If an animal is kept from contact with all conspecifics for an extended time an "isolation stress syndrome" develops; if the isolation is started at a young enough age, then antisocial behaviors become permanent (see for example Harlow & Harlow, 1965). Of course our kittens with monocular experience in isolation had only short-term separation anxiety--they were never kept away from other cats long enough for isolation stress to develop.

We tested only one kitten (M263) conditioned with a sibling; it had a shift index of 0.80. It is possible that a sibling could substitute nearly as well as the mother to reduce anxiety, provide an interactive visual stimulus, and promote OD shift.

Enriched and impoverished environments.

If we place objects near enough that it can explore them, then we are enriching a kitten's environment. Rosenzweig, Bennett & Diamond (1972a&b) put rats in enriched (EC) or impoverished (IC) environments and found that occipital cortex was 10% heavier, 6% thicker and had synapses "longer" but less numerous (also see Greenough, 1976). Even if EC rats, in their world of toys and social contacts, were blinded or left in darkness they still showed differential brain weight gains in occipital cortex. Nor are these strictly *developmental* changes: the results are commonly obtained with *adult* rat pairs in the EC and IC environments. However, the differences take less time to produce with younger the animals. When Malkasian and Diamond (1971) raised *neonatal* rat pups in EC's, they found larger differences in occipital cortex thickness between EC pups and pups raised with their mothers in IC's. An experiment by Ferchmin et al. (1975) showed that *participation* in the EC was important for cerebral changes: they placed an IC cage in the middle of an EC area, where the IC rats could have passive viewing of the EC hurly-burly. These activity-isolated rats showed no significant differences from completely isolated rats.

Beaulieu & Colonnier (1985) reported on the consequences of EC and IC rearing of kittens (from weaning until 8 mo. of age). They found a 45% reduction in 'flat-symmetric' synapses in the visual cortex of EC cats, and suggested that visual experience may prune GABA-dependent inhibition by eliminating such synapses.

Age-dependent motor activity.

A kitten's age determines to a large extent how it relates to its environment, and its mother. For example, whether or not a kitten is weaned must greatly influence the quality of separation anxiety. Hirsch (1986) divides the kitten's development of visually guided behavior

to categorize luminance levels is a convenience justified in Method.

into three stages. By the end of the second stage, around seven weeks of age, weaning is usually complete, and in the third stage a kitten begins "...to seek interactions with stimuli and objects outside the home cage." From Table I it can be calculated that our kittens began their week of monocular experience at an average age of 38 days (range: 23 - 51 days), just at the time of weaning. An inspection of Table I shows no positive effect of age *per se* on strength of ocular dominance shift. Perhaps those kittens who began monocular experience after weaning were old enough that ocular dominance shift proceeded at a slower rate (Olson & Freeman, 1980a) in spite of their being somewhat more independent of their mothers.

Further work.

Both isolation stress and separation anxiety are accompanied by neurochemical changes--for example Panksepp and colleagues have evidence that opiates mediate separation anxiety. Morphine reduces and naloxane increases distress vocalization after separation (see Panksepp *et al.*, 1985). One direction for further research on conditions required for OD shift in monocularly deprived kittens would be testing the pharmacological dependence of OD shift on opiates and their antagonists, infusing drugs into visual cortex in ways that have proven effective for noradrenergic and cholinergic agents (Bear et al., 1983; Bear & Singer, 1986). This direction would link the internal and external factors outlined in the first paragraph of Introduction.

Another direction for further research, and one which would not involve altering chemical balances in cerebral cortex, would be investigation of the near visual world's quality for a kitten. We have in mind an environment in which a kitten's movements could be detected, and such detection then be used to modulate the illumination of its environment. If, for example, movement caused illumination to cease until the animal held still for a required time, then a kitten could be deprived of *optic flow* experience, while still able to view all it wanted if it sat still. One kitten, could, in fact, act as its own control if "alternating occlusion" (Hubel & Wiesel, 1965) were used to control which eye viewed the world when optic flow were permitted. Such an environment would also provide another demonstration of Hirsch's (1986) three stages of visuo-motor development and would show how a kitten's motor activity increases dramatically at the start of the critical period.

References

Bear, M.F. & Daniels, J.D. (1983) The plastic response to monocular deprivation persists in kitten visual cortex after chronic depletion of norepinephrine. *J. Neurosci.* **3,** 407-416.

Bear, M.F., Paradiso, M.A., Schwartz, M., Nelson, S.B., Carnes, K.M. & Daniels, J.D. (1983) Two methods of catecholamine depletion in kitten visual cortex yield different effect on plasticity. *Nature* **302,** 245-47.

Bear, M.F. & W. Singer (1986) Modulation of visual cortical plasticity by acetylcholine and noradrenaline. *Nature* **320,** 172-76.

Beaulieu, C. & Colonnier, M. (1985) The differential effect of impoverished and enriched environments on the number of 'round asymmetric' and 'flat symmetric' synapses in the visual cortex of cat. *Soc Neurosci. Abst.* **11,** 226.

Berman, N. & Daw, N.W. (1977) Comparison of the critical periods for monocular and directional deprivation in cats. *J. Physiol.* **265,** 249-259.

Bisti, S., Clement R., Maffei L., & Mecacci, L. (1977) Spatial frequency and orientation tuning curves of visual neurons in the cat: Effects of mean luminance, *Exp. Brain Res.* **27**: 335-345.

Boynton, R.M. (1966) Vision. in Sidowski, J.B. (ed.), *Experimental Methods and Instrumentation in Psychology.* McGraw Hill, New York. 273-329.

Cooper, L.N (1985) A model for the development of neurons in the visual cortex. in Rose, D. & Dobson, V.B. (eds.) *Models of the Visual Cortex* John Wiley & Sons, Chichester. 164-171.

Cynader, M., Berman N., & Hein A., (1973) Cats reared in stroboscopic illumination: Effects on receptive fields in visual cortex. *Proc. Nat. Acad. Sci. USA* **70,** 1353-1354.

Daniels, J.D., Pressman, E., Schwartz, M., Nelson, S.B. & Kraus, D.J. (1984) Effects of luminance and flicker on ocular dominance shift in kitten visual cortex. *Exp. Brain Res.* **54,** 186-190.

Daniels, J.D. & Saul, A.B. (1986) One week's monocular experience in 16 Hz strobe illumination is adequate to promote complete ocular dominance shift in monocularly deprived kittens. *Invest. Ophthalmol. Vis. Sci. (suppl.)* **27,** 245.

Daw, N.W., Berman, N.E.J. & Ariel M. (1978) Interaction of critical periods in the visual cortex of kittens. *Science* **199,** 565-567.

Ferchmin, P.A., Bennett E.L. & Rosenzweig, M.R., (1975) Direct contact with enriched environments is required to alter cerebral weights in rats, *J. Comp. Physiol. Psyc.* **88,** 360-367.

Frisby, J.P. (1979) *Seeing: Illusion, Brain and Mind.* Oxford Univ. Press, Oxford.

Garrett, Mary Anne (1981) Vision restricted to one small, randomly flashing spot: Effects on development of kitten area 17 neurons. *Master's Thesis,* Brown University, Providence, RI.

Gibson, J.J. (1979) *An Ecological Approach to Visual Perception*; Houghton Mifflin, Boston.

Greenough, W.T., (1976) Enduring brain effects of differential experience and training, in Rosenzweig, M.R. & E.L. Bennett (eds.), *Neural Mechanisms of Learning and Memory*; MIT Press, Cambridge, MA. 255-278.

Halliday, D. & Resnick, R. (1981) *Fundamentals of Physics, 2nd Edition.* John Wiley & Sons, New York.

Hammond, P. & C.R. James, (1971) The purkinje shift in cat: Extent of the mesopic range, *J. Physiol.* **216,** 99-109.

Harlow, H.F. & Harlow, M.R., (1965) The affectional systems, pp. 287-334 in Schrier, A.M., Harlow H.F. & Stollnitz, F. (eds.), *Behavior of Nonhuman Primates, Vol. II,* Academic Press, New York.

Hirsch, H.V.B. (1986) The tunable seer: Activity-dependent development of vision. in Blass, E.M. (ed), *Handbook of Behavioral Neurobiology, Vol. 8, Developmental Psychobiology and Developmental Neurobiology.* Plenum Press, New York. 237-295.

Hirsch, H.V.B. & Spinelli, D.N. (1971) Modification of the distribution of receptive field orientation in cats by selective visual exposure during development. *Exp. Brain Res.* **12,** 509-527.

Hubel, D.H. & Wiesel, T.N. (1962) Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol.* **160,** 106-154.

Hubel, D.H. & Wiesel, T.N. (1965) Binocular interaction in striate cortex of kittens reared with artificial squint. *J. Neurophysiol.* **28,** 1041-1059.

Kolb, H. & Famiglietti, E.V. (1974), Rod and cone pathways in the inner plexiform layer of cat retina. *Science* **186,** 47-49.

Levick, W.R., "Another tungsten microelectrode", *Med. Biol. Eng. 10*: 510-515 (1972).

Malkasian, D.R. & Diamond, M.C. (1971) The effects of environmental manipulation on the morphology of the neonate rat brain. *Int. J. Neurosci.* **2,** 161-170.

Marr, D. (1982) *Vision.* W.H. Freeman & Co., San Francisco.

Mouat, G.S.V. (1985) Photoreceptor inputs to cat lateral geniculate nucleus cells, *Exp. Brain*

Res. **59**: 242-248.

Nelson, S.B., Schwartz, M.A. & Daniels, J.D. (1985) Clonidine and cortical plasticity: Possible evidence for noradrenergic involvement. *Dev. Brain Res.* **23,** 39-50.

Olson, C.R. & Freeman, R.D. (1975) Progressive changes in kitten striate cortex during monocular vision. *J. Neurophysiol.* **38,** 26-32.

Olson, C.R. & Freeman, R.D. (1980a) Profile of the sensitive period for monocular deprivation in kittens, *Exp. Brain Res.* **39,** 17-21.

Olson, C.R. & R.D. Freeman (1980b) Rescaling the retinal map of visual space during the growth of the kitten's eye. *Brain Res.* **186,** 55-65.

Olson, C.R. & Pettigrew, J.D. (1974) Single units in visual cortex of kittens reared in stroboscopic illumination. *Brain Res.* **70,** 189-204.

Orban, G.A., Kennedy , H. & Maes, H. (1980) Functional changes across the 17-18 border in the cat. *Exp. Brain Res.* **39,** 177-186.

Panksepp, J., Siviy, S.M. & Normansell, L.A. (1985) Brain opioids and social emotions. in Reite & Field (eds.) *The Psychobiology of Attachment and Separation* Academic Press, New York. 3-49.

Pettigrew, J.D. & Freeman, R.D. (1973) Visual experience without lines: Effect on developing cortical neurons. *Science* **182,** 599-601.

Ramoa, A.S., Freeman, R.D. & A. Macy, A. (1985) Comparison of response properties of cells in the cat's visual cortex at high and low luminance levels, *J. Neurophysiol.* **54**: 61-72.

Rauschecker, J.P. & Singer, W. (1981) The effects of early visual experience on the cat's visual cortex and their possible explanation by Hebb synapses, *J. Physiol.* **310,** 215-240.

Reite, M. & Field. T., eds. (1985) *The Psychobiology of Attachment and Separation* Academic Press, New York.

Riggs, L.A. (1971) Vision. in Kling, J. & Riggs, L.A. (eds.); *Woodworth's Experimental Psychology, 3rd Edition*; Holt, Rinehart and Winston, Inc., New York. 273-314.

Rosenblatt, J.S. & Siegel, H.I. (1981) Factors governing the onset and maintenance of maternal behavior among nonprimate mammals: The role of hormonal and nonhormonal factors, pp. 13-76, in *Parental Care in Mammals*: Gubernick & Klopter (eds.) Plenum Press, New York.

Rosenzweig, M.R., Bennett, E.L. & Diamond, M.C. (Feb. 1972a) Brain changes in response to experience, *Sci. Am.* **226,** 22-29.

Rosenzweig, M.R., Bennett, E.L. & Diamond, M.C. (1972b) Chemical and anatomical plasticity of brain: replications and extensions. in Gaito, J. (ed.), *Macromolecules and Behavior, 2nd Edition*, Appleton-Century-Crofts, New York. 205-277.

Sanseverino, E.R., Galletti, C. & Squatrito, S. (1979) Stimulus-response function at several levels of background luminance, in the cat visual areas 17 and 18. *Experientia* **35,** 358-359.

Steinberg, R.H., Reid M. & Lacy P.L. (1973) The distribution of rods and cones in the retina of the cat *(felis domesticus). J. Comp. Neurol.* **148,** 229-248.

Stryker, M.P. & Sherk, H. (1976) Modification of cortical orientation selectivity in the cat by restricted visual experience: A reexamination. *Science* **190,** 904-905.

Stryker, M.P., Sherk, H., Leventhal, A.G. & Hirsch, H.V.B. (1978) Physiological consequences for the cat's visual cortex of effectively restricting early visual experience with oriented contours. *J. Neurophysiol.* **41,** 896-909.

Tusa, R.J., L.A. Palmer & A.C. Rosenquist (1978) The retinotopic organization of area 17 (striate cortex) in the cat. *J. Comp. Neurol.* **177,** 213-236.

Van Sluyters, R.C. & Blakemore, C. (1973) Experimental creation of unusual neuronal properties in visual cortex of kittens. *Nature* **246,** 506-08.

Wiesel, T.N. & Hubel, D.H. (1963) Single-cell responses in striate cortex of kittens deprived of vision in one eye. *J. Neurophysiol.* **26,** 1003-1017.

Figure Captions

Table I

Data summary for the 30 kittens used in the study. The letter preceding kitten's identification number indicates its mother. Litters were transferred to the darkroom between 13-16 days of age, just after time of eye opening.

Under *Conditioning Environment* we note luminance in milli-foot Lamberts, and whether the kitten had its mother with it and whether a mobile, as shown in Fig. 1, was suspended outside the cage. At its "far" position the mobile was 150 cm away from the front of the cage; at its "close" position it was 75 cm away.

Under *Units* we list the unresponsive sites, as determined by criteria discussed in Methods. Only visually responsive units are used in the Ocular Dominance Shift Index, defined below.

$$\text{OD Shift Index} = \frac{\text{total units the TWO categories dominated by open eye}}{\text{total all units classified for OD}}$$

Thus, an OD Shift Index at a maximum of 1.0 describes a complete OD shift toward the opened eye, but 0.0 could indicate either binocularity or a shift toward the closed eye.

The right-most column indicates which of the subsequent figures illustrates the ocular dominance histogram for each group of kittens.

Figure 1

The conditioning room, and it possible arrangements. The cage had a shelf in it, and the "walls" of the cage were made of chicken wire. Four spotlights could have their direction and intensity varied to highlight a mobile suspended outside the cage, and/or the cage's inside. A fan under the cage could rotate the mobile. A stuffed animal (in this case a rabbit) could be suspended from the cage roof by elastic thread. In some cases, as indicated in Table I, the MD kitten's mother would accompany the kitten during its week of monocular experience.

Figure 2

Ocular dominance (OD) histogram of 362 area 17 units from nine MD kittens each of which got to view the mobile in dim (scotopic) illumination **alone, without mother, sibling or stuffed animal.** In some cases the mobile was close, in other cases it was far; in some cases the fan was on, in others it was off. As can be seen from the OD Shift Index for each kitten, and the overall histogram, these arrangements made no significant difference--there was virtually no shift for this group. The OD shift index average is 0.40.

The seven category scheme of (Hubel & Wiesel (1962) was used. OD category R is for cells driven exclusively by the open (right) eye; category L is for cells driven exclusively by the closed (left) eye. The other five categories indicate different degrees of binocularity, with the middle column representing cells which responded equally (within a factor of two) to each eye. U (Unclassifiable) denotes cells visually responsive but too sluggish or variable to be categorized reliably. NV (Non-visual) corresponds to the unresponsive sites in Table I. (The U and NV percentages are calculated as a fraction of the 328 OD-units.)

Animal G318 and G319, the last two of the group, could conceivably have been placed with the Fig. 5 group, because their sawdust illumination was so much more than the others used for Fig. 2. However, for all the kittens listed, the mobile's illumination was the same. For G318 & 319 the sawdust inside the cage was brighter because the normally opaque roof was replaced with a translucent screen.

Figure 3

OD histogram for three dark-reared kittens. This control group had OD shift index average of 0.23. Note the many (55) unresponsive recording sites. Categories for ocular dominance as defined in Fig. 2's caption.

Figure 4

OD histogram for three kittens with monocular experience (ME) *alone*, in brighter (photopic) illumination. This group had a good shift, with an index average of 0.72. Categories for ocular dominance as defined in Fig. 2's caption.

Figure 5

OD histogram for three kittens given ME **alone** in moderate (mesopic) illumination, without the mobile present. In spite of the increased illumination, the OD shift index (0.17) remains close to that obtained with the dim, isolated group (Fig. 2). Animals G318 and G 319

from the Fig. 2 group also had "mesopic" illumination of their sawdust, like the others in Fig. 5, but for G318 and G319 the mobile was present, and it was not for the others in the Fig. 5 group.

Figure 6

OD histogram for five kittens who had ME in dim illumination, **with their mothers**. The mobile was present in all cases. This group can be compared directly with the Fig. 2 group. With the mother present the OD shift index is doubled, to 0.83, and a clear shift is apparent from the histogram. The one kitten (C358) with the lowest shift index died after only 10 units were recorded. Another kitten, M263, who was accompanied by a sibling, could have been grouped with the two represented in Fig. 8. Note that M263 received 10 days of monocular experience instead of the usual 7, but its shift index was still one of the lowest of the group.

Figure 7

OD histogram for three kittens given moderate (mesopic) ME **with their mothers.** The mobile was removed from view. A virtually complete OD shift occurred (index of 0.95). These kittens can be compared directly with those represented in Fig. 5. Again, the only difference was the presence of the mother for the Fig. 7 group.

Figure 8

OD histogram for two MD kittens conditioned with a stuffed rabbit and allowed to view a dimly-lit mobile. The OD shift index, 0.69, is less than either group conditioned with the mother, and less than the 0.80 of M263, who was conditioned with a sibling.

Figure 9

Thirty eight units from one kitten given a week of ME with its mother in very dim illumination (0.01 mFL). OD shift index is only 0.40. Thus an order of magnitude reduction in illumination appears to eliminate any positive effect the presence of the mother has in promoting OD shift.

Figure 10

Forty one units from one MD kitten, P455, whose mother was visible, but kept in another chicken wire cage, separated by 75 cm from the kitten's conditioning cage. The OD shift index of 0.64 is greater than all but one of the indices from the kittens in the Fig. 2 group, who viewed a mobile at a distance. Note that P455 was also the oldest kitten we recorded from.

TABLE I

DATA BASE

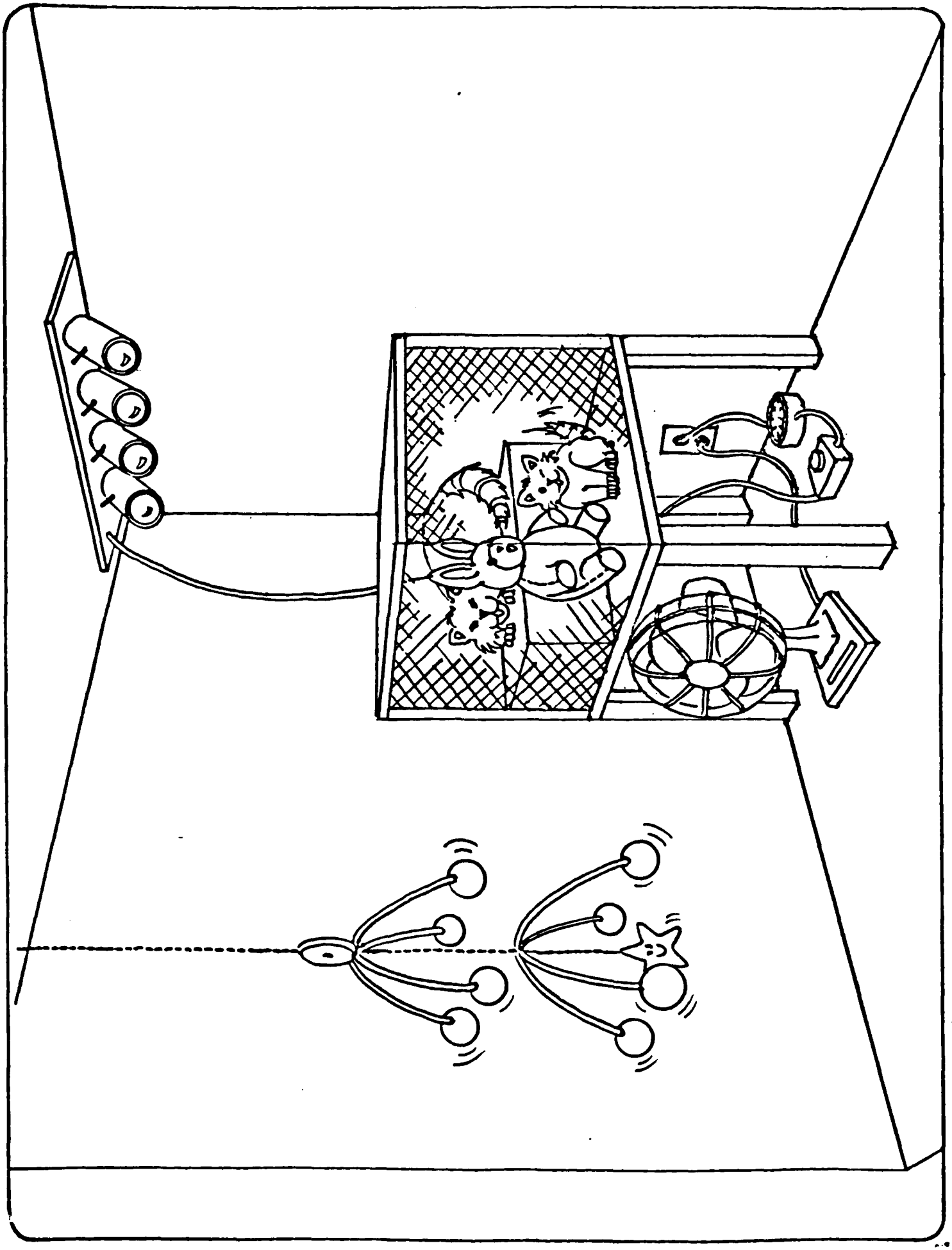
KITTEN id	sex	Conditioning: Environment: Luminance of Cage Sawdust	Mobile	Companion	Timing: Onset	Duration	At Recording: Age days	Wt.gm.	Units: Vis. Resp.	Unresp.	OD Shift Index	Fig. #
G287	M	0.3 mfL	far (s)	none	37 days	9 days	46	450	46	1	.60	
G288	F	0.3 mfL	far	"	39	13	52	360	42	2	.28	
G289	F	"	far (s)	"	40	12	52	400	44	7	.38	
G290	F	"	far	"	46	12	58	360	23	0	.67	
I302	F	"	close	"	39	10	49	500	43	0	.25	2
C307	F	"	close	"	28	7	35	400	46	0	.54	
K312	F	0.3 mfL	close	"	28	7	35	400	49	2	.23	
G318	F	5.0 mfL ǂ	close	"	44	7	51	280	26	0	.42	
G319	M	15.0 mfL ǂ	close	"	51	7	58	450	43	1	.40	
I303	M	Dark-rearing		Mom and	14	42	56	500	53	18	.26	
F67	F	"		Siblings	15	22	37	430	51	25	.20	3
G72	F	"		"	14	26	40	400	43	12	.23	
N350	F	37 mfL ǂ	none	none	33	7	40	430	21	0	.70	4
F332	F	* 70 mfL ǂ	"	"	40	7	47	590	40	0	.74	
M344	F	* 70 mfL ǂ	"	"	38	7	45	425	35	3	.71	
F333	F	15 mfL ǂ	none	none	42	7	49	430	46	0	.27	5
M342	F	15 mfL ǂ	"	"	31	7	38	400	49	7	.50	
N351	F	15 mfL ǂ	"	"	40	7	47	600	20	2	.65	
M263	M	0.5 mfL #	far	Sibling	34	10	44	392	33	4	.80	
M355	F	0.9 mfL	"	Mom	37	7	44	330	27	7	.80	
M356	M	0.9 mfL	"	"	41	7	48	450	23	4	.85	6
C358	F	0.3 mfL	"	"	33	7	40	400	9	1	.38	
C360	M	0.3 mfL	"	"	44	7	51	690	38	2	.97	
N352	M	15 mfL	none	Mom	49	7	56	620	32	0	1.00	
M353	M	15 mfL	none	"	23	7	30	350	25	1	.85	7
M354	F	15 mfL	none	"	30	7	37	450	45	0	1.00	
C359	F	0.90 mfL	close	toys	37	7	44	350	17	1	.75	
C361	F	0.30 mfL	close	toys	51	7	58	650	24	0	.63	8
E347	M	0.01 mfL #	none	Mom	41	7	48	765	38	0	0.40	9
P455	M	0.9mfL	Mom	none	54	7	61	500	40	1	0.64	10

Normal metal bar cage, 3m from source

* Argon-tube used as illumination.

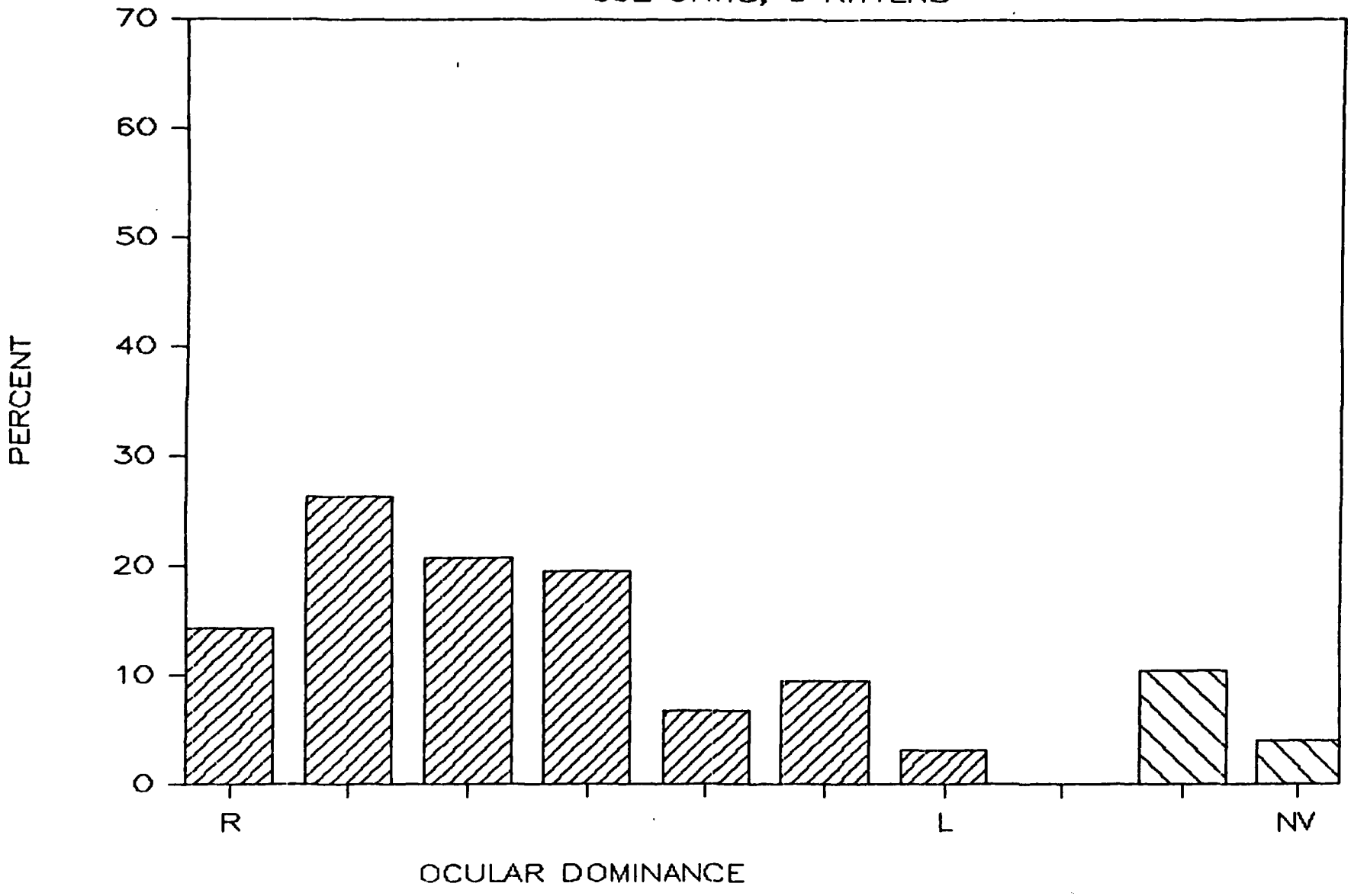
(s) Mobile Stationary

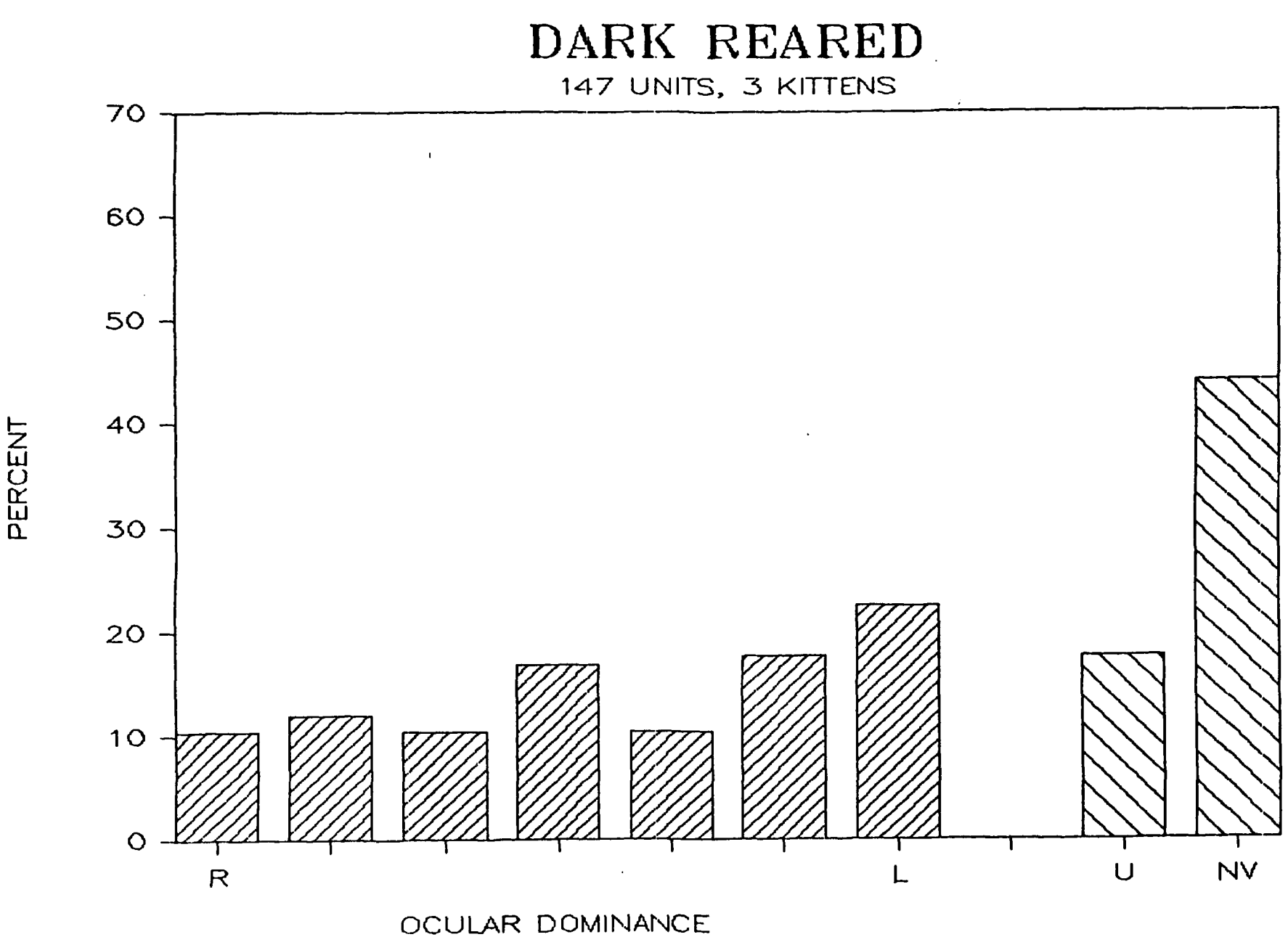
ǂ Diffuser instead of occluder on cage top. See Figure 1.



ISOLATED, SCOTOPIC, MOBILE

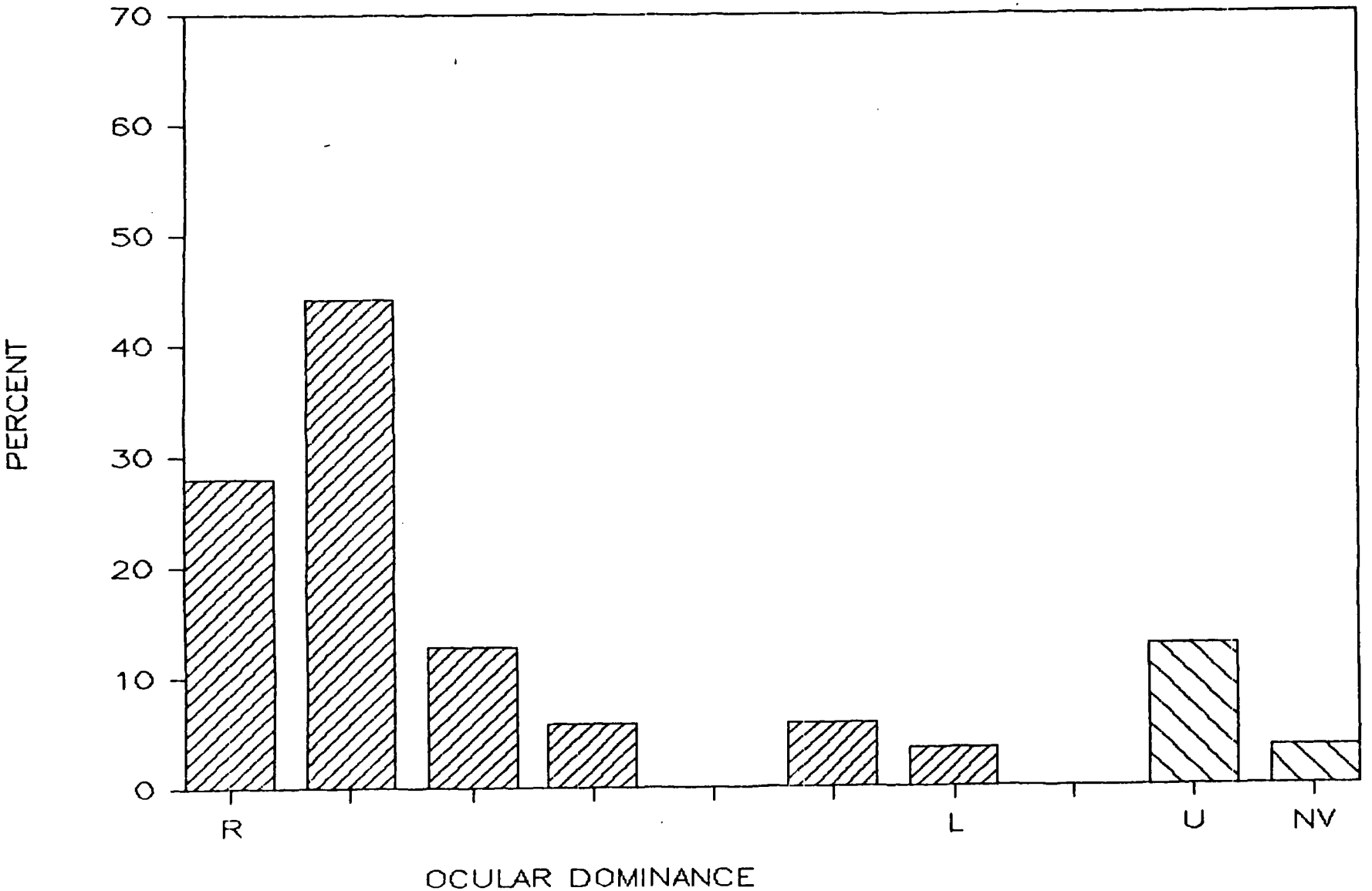
362 UNITS, 9 KITTENS




DARK REARED
147 UNITS, 3 KITTENS
70
60
50
40
30
20
10
0
PERCENT
R
L
U
NV
OCULAR DOMINANCE

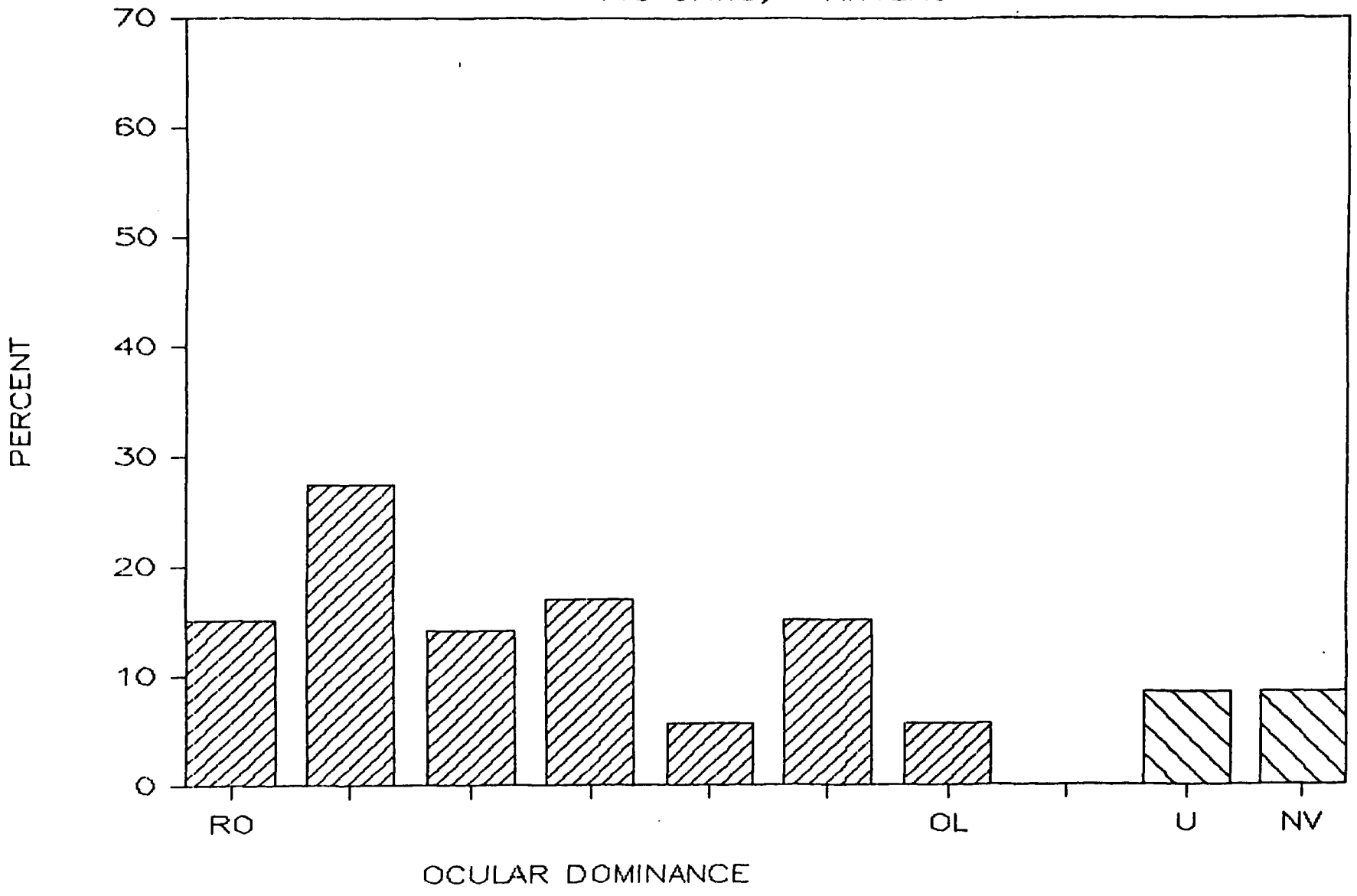
ISOLATED, PHOTOPIC, NO MOBILE

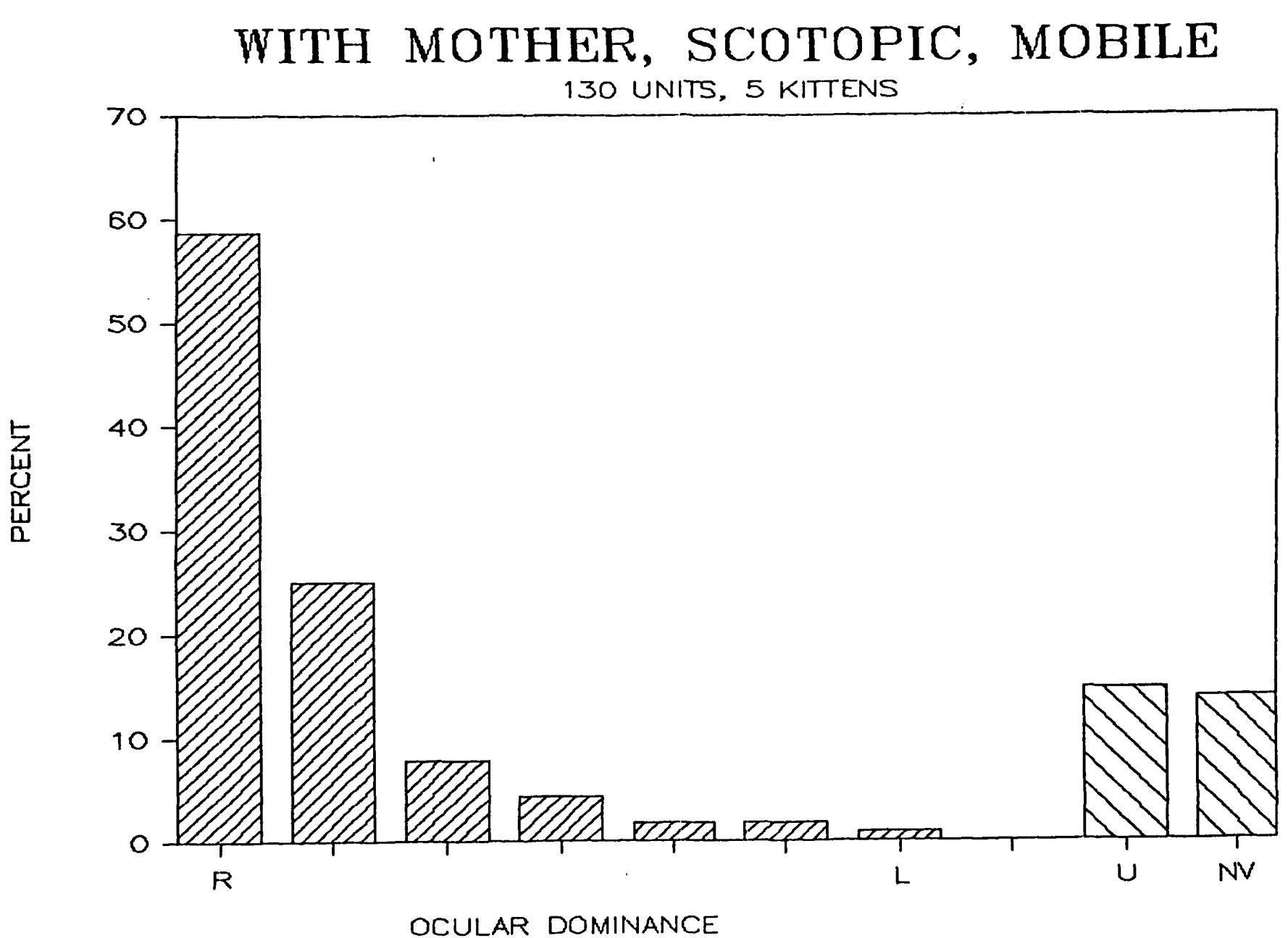
96 UNITS, 3 KITTENS



ISOLATED, MESOPIC, NO MOBILE

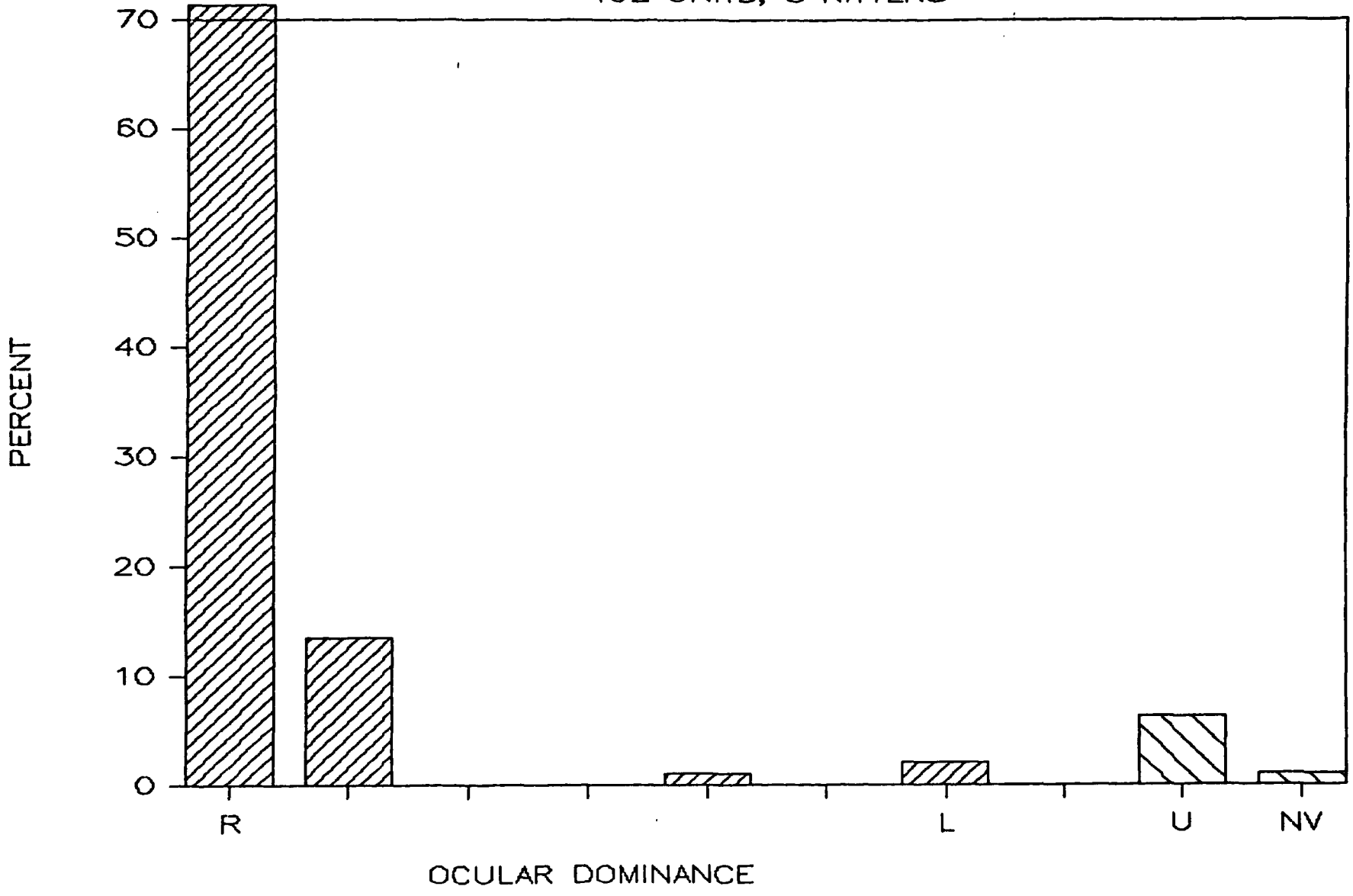
115 UNITS, 3 KITTENS




WITH MOTHER, SCOTOPIC, MOBILE
130 UNITS, 5 KITTENS
PERCENT
70
60
50
40
30
20
10
0
R
L
U
NV
OCULAR DOMINANCE

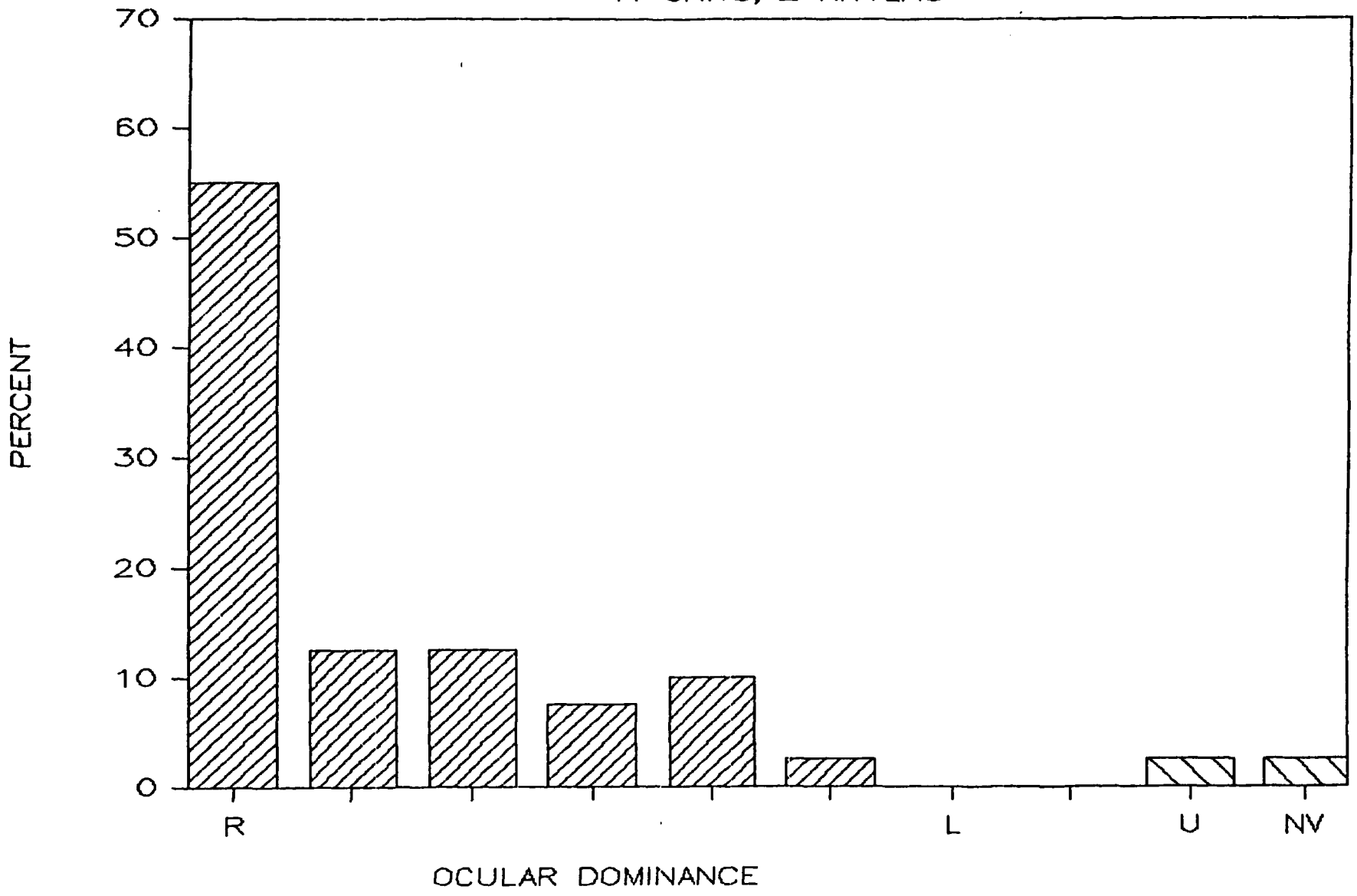
WITH MOTHER, MESOPIC, NO MOBILE

102 UNITS, 3 KITTENS



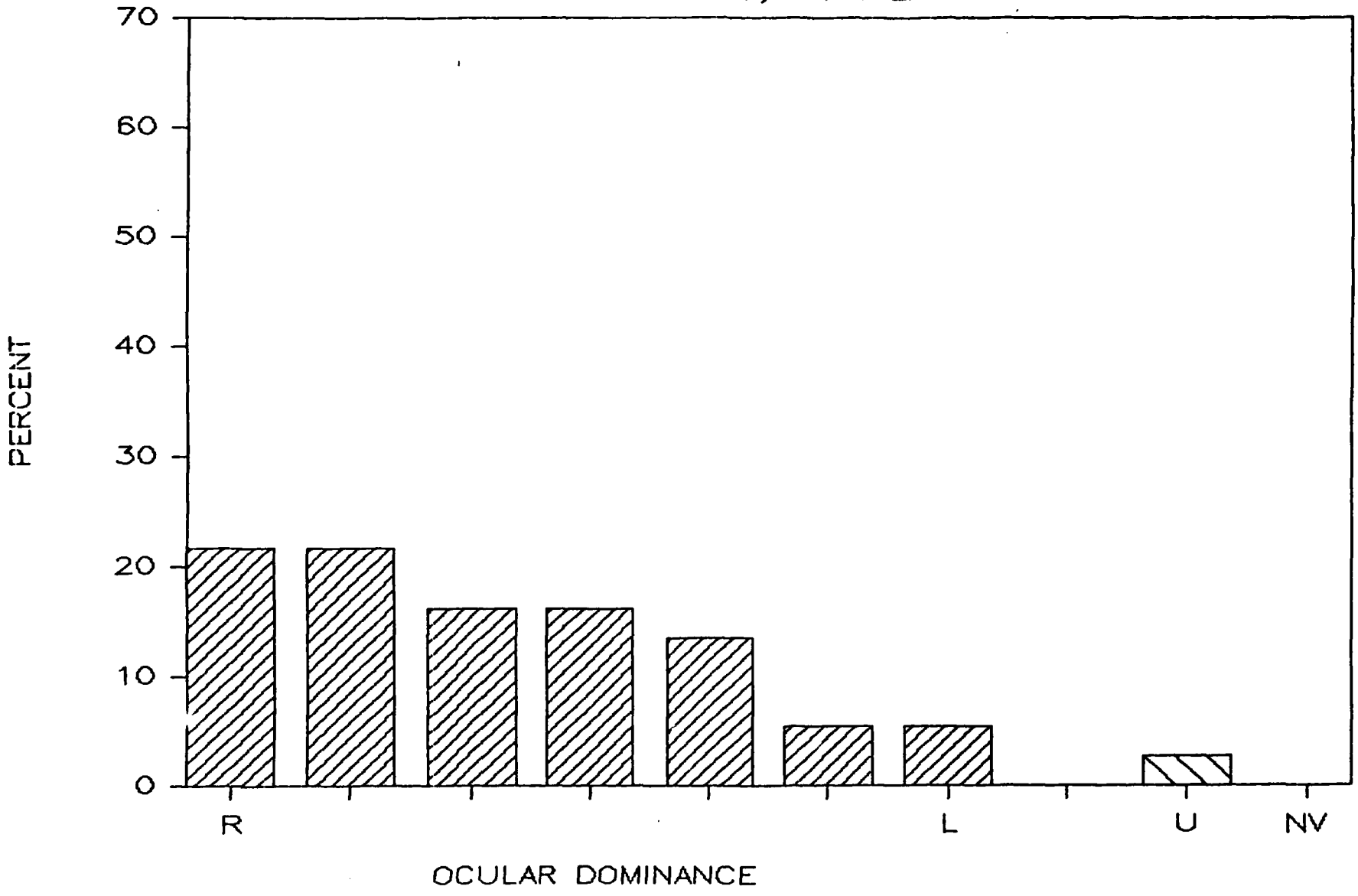
WITH STUFFED RABBIT, SCOTOPIC, MOBILE

41 UNITS, 2 KITTENS



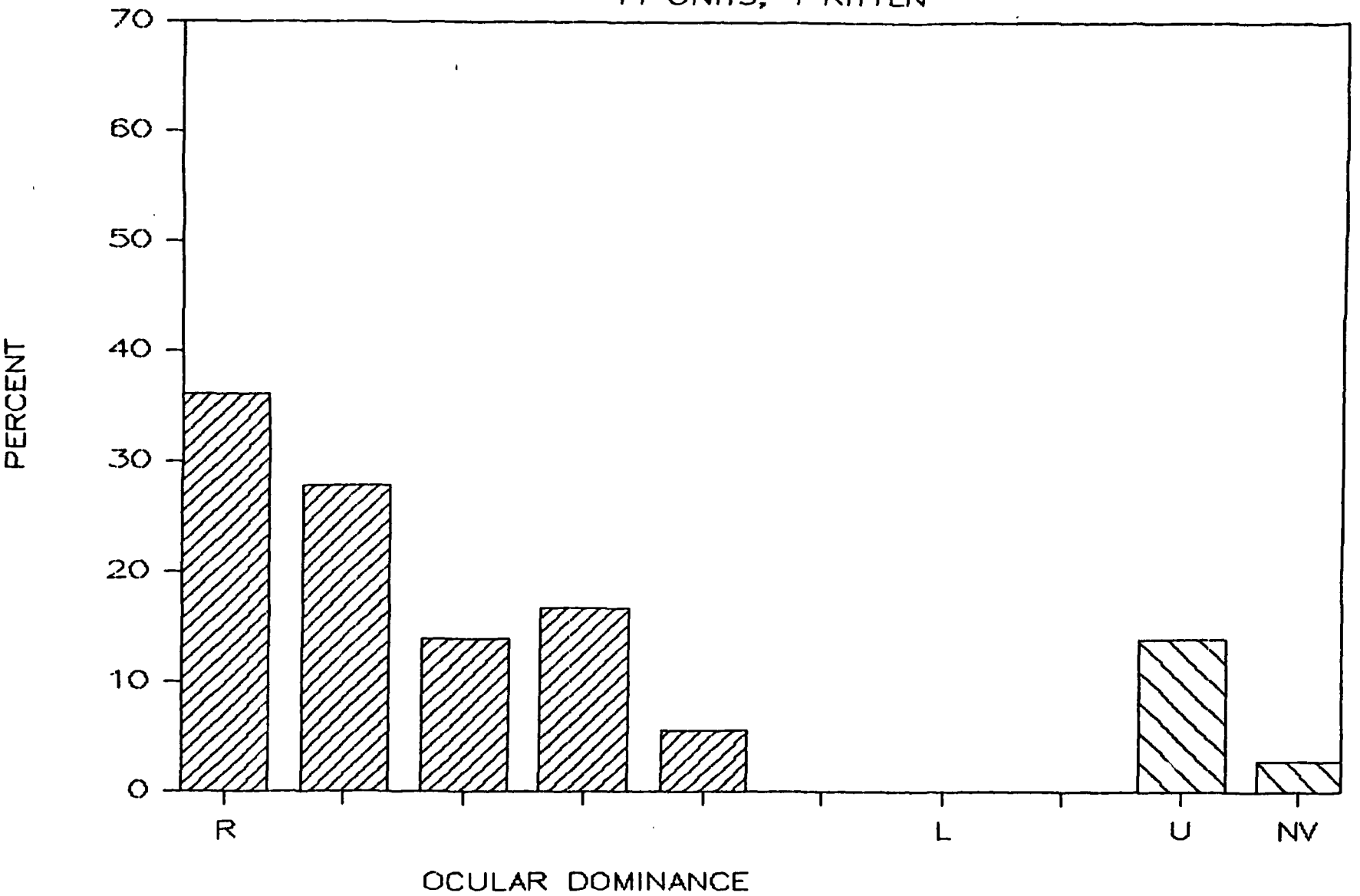
VERY DIM, SCOTOPIC, WITH MOTHER

38 UNITS, 1 KITTEN



MOTHER IN PLACE OF MOBILE

41 UNITS, 1 KITTEN



END

1-87

DTIC