Monkey	Trials (No.)					Tactile and visual: errors in 80 trials in light and dark
	Tactile			Visual		
	C vs. S	Cone vs. P	P vs. cone	P. vs. cone	Cone vs. P	
1	90	0		20		3
2	210		0		40	4
3	80		40		20	5
3a	130		680+			
4	170	50		60		1

different test objects and a group of naive monkeys.

Our subjects, four adolescent rhesus monkeys, were trained in standard apparatus with standard procedures for visual and tactile object discrimination learning (2). On all tasks 40 trials were given daily, 5 days a week, until each animal made 20 or fewer errors in 200 consecutive trials (Table 1).

All animals were first taught in the dark to perform a simple discrimination task (cylinder and sphere) merely in order to adapt them to tactile training. All were then required to discriminate in the dark between cone and pyramid; two were rewarded for choosing the cone; the other two, for choosing the pyramid. The animals then learned to make the opposite discrimination in the light: that is, those trained to select the cone in the dark were trained to select the pyramid in the light, and vice versa. Finally, all were given 80 trials of pseudo-random alternation between light and dark, with rewards as during training.

We can evaluate the results (Table 1) in two ways: First, we can compare learning scores for the reversed discrimination in a *different* sense modality with learning scores for a reversed discrimination in the *same* modality. These animals required more trials (ratio, 1.6:1) to learn the reversed discrimination by vision than were required for original tactile learning. In contrast, another group of eight animals required more trials (ratio, 75:1) to learn the reversed discrimination by touch than the original discrimination by touch, again with the cone and pyramid (3). Secondly, we can note that the performance of all four animals was 90-percent correct or better when retention of both habits was tested during 80 trials in the light and dark.

Our results imply that tactile and visual learning proceed independently in the monkey, as was shown earlier in two classes of experiment: First, work

was done on cross-modal transfer of training, when learning in a single sense modality may or may not lead to improved learning of the *same* (not *opposite*) discrimination in a second modality; such experiments have generally failed to produce evidence of significant cross-modal effects (4). Secondly, work was done on concurrent learning in two sense modalities, when sensory inflow through two sense modalities is made available during learning, but tests are subsequently made with the inflow restricted to a single modality; results were inconclusive (5).

Our findings show, first, that transfer of training did not take place between sense modalities in our monkeys, since the reversed discrimination was learned almost as readily by vision as the origi-

nal was learned by touch. Secondly, during training in the light, our monkeys failed to make use of the tactile information available to them as a result of their grasping the objects that were selected on the basis of vision; when subsequently tested on 40 trials in the dark, they responded in accordance with the original tactile training and not in accordance with their subsequent visual (and tactile) experience (6). Therefore, from two lines of evidence we conclude that tactile and visual learning take place in independent functional systems.

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6. Errors made by all animals during the 80 tactile and visual test trials were made in the dark on tactile trials. This observation may reflect either simple forgetting of the first-learned task or direct interference (of a minimal kind) between tactile and visual learning.
7. We thank G. D. Dawson for facilities and encouragement and the Medical Research Council for financial support.

9 March 1966 ∎

Carotid Body Chemoceptors: Physiological Role in Buffering Fall in Blood Pressure during Sleep

Abstract. *In cats whose aortic nerves were severed subsequent deafferentation of the carotid body chemoceptors (the carotid sinus baroceptors remaining intact) did not change arterial pressure during wakefulness or light sleep, but the falls in pressure during deep sleep were markedly exaggerated. Subsequent baroceptive denervation did not modify the hypotensive effect.*

Regarding circulatory changes accompanying the wakefulness-sleep cycle of the cat, we reported earlier (1) that the falls in blood pressure that occur during deep sleep (with a desynchronized electroencephalogram and bursts of rapid eye movements) are much greater after bilateral sino-aortic deafferentation: in several deafferented cats arterial pressure fell so low that episodes of transient cerebral ischemia occurred. Since in these experiments both baro- and chemoceptive fibers from the sino-aortic areas were interrupted, we could not decide whether it was abolition of baroceptive or of chemoceptive reflexes that caused such striking exaggeration of the hypotensive effect of

deep sleep. The respective roles of the two types of receptors in controlling circulation during sleep could only be assessed by selective interruption of one type of afferent fibers while the other was left largely intact. We now report such experiments.

In all cats systolic and diastolic pressures were recorded throughout the wakefulness-sleep cycle from a permanently cannulated femoral artery; electroencephalogram, cervical electromyogram, and eye movements were also monitored (1). A first group of three cats were subjected to sino-aortic denervation in three stages, each stage being followed by a recording session. The first stage consisted in bilateral section

of the aortic nerves (2), while innervation of the carotid bifurcation was left intact. The second stage consisted in selective bilateral destruction, by thermocoagulation, of the carotid body chemoceptors; success was assessed by disappearance of the pressor and respiratory response to injection of KCN (15 μg) into each sinus. Persistence of a large pressor response to common carotid occlusion indicated that baroceptors were mostly spared. The third stage of denervation consisted in bilateral section of the carotid sinus nerves, which added baroceptive to chemoceptive deafferentation.

Each of the three recording sessions took place a few days after each denervation stage, when the animals had fully recovered from both operation and anesthesia. In each session the arterial pressure of the unrestrained cat was continuously monitored during ten consecutive light sleep–deep sleep cycles. Differences between values recorded in the three experimental conditions (carotid sinus area intact, selective deafferentation of the chemoceptors, total deafferentation) were evaluated by analysis of variance, with multiple classification (3).

The mean values of all measurements in the three cats in each experimental condition are plotted in the left half of Fig. 1. As we reported earlier (1), when the carotid sinuses were intact, falls in systolic and diastolic pressures were moderate during light sleep but greater during deep sleep. Selective chemoceptive deafferentation, sparing most carotid sinus baroceptors, did not significantly modify the blood pressures recorded during wakefulness or light sleep or at the onset of deep sleep, but much larger falls—to much lower absolute values—were invariable during deep sleep. Changes induced by the selective denervation were highly significant statistically (p < .001). Final completion of carotid sinus denervation by baroceptive deafferentation did not change quantitatively the fluctuations in blood pressure characteristic of sleep.

A second group of three cats were subjected to selective baroceptive, rather than chemoceptive, deafferentation and studied in two stages: (i) after bilateral section of the aortic nerves and selective denervation of the baroceptors in the carotid sinus areas. Selective baroceptive deafferentation was confirmed by negligible pressor responses to carotid occlusion, associated with persistence of pressor and respira-
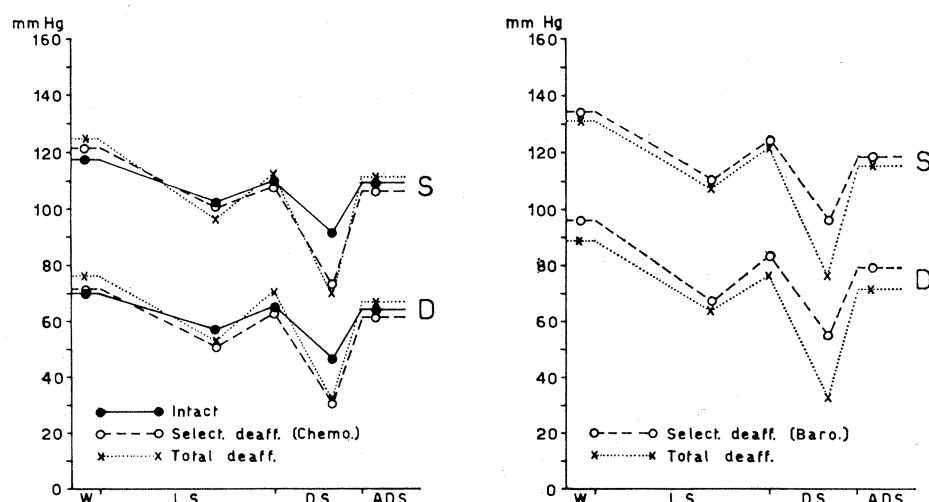

Fig. 1. Changes in systolic (S) and diastolic (D) blood pressure during the wakefulness-sleep cycle. Each mark represents the mean of 30 measurements (ten in each of three cats) selected from a continuous blood-pressure record under the following circumstances (left to right): quiet wakefulness (W), light sleep (LS; lowest measured values), onset of deep sleep, deep sleep (DS; lowest measured values), and after deep sleep (ADS). (Left) Animals studied in three stages: (i) with intact innervation of the carotid bifurcation (solid circles); (ii) after selective deafferentation of carotid body chemoceptors (hollow circles); and (iii) after subsequent total denervation of the carotid bifurcation (crosses). (Right) Animals studied (i) after selective deafferentation of carotid sinus baroceptors (hollow circles), and (ii) after total deafferentation of the carotid bifurcation (crosses). Note that in both groups of animals only chemoceptive deafferentation, either selectively performed (left) or added to baroceptive denervation (right), markedly exaggerates the falls in blood pressure occurring during deep sleep.

tory responses to locally injected KCN. After a few days, a blood pressure–recording session was performed during natural sleep according to our usual procedures, and followed by (ii) completion of the denervation by the cutting of both carotid sinus nerves. A second recording session was performed 5 to 7 days later.

The right half of Fig. 1 shows that, when all baroceptive afferents had been cut (the carotid body chemoceptors remaining intact), the fall in blood pressure during deep sleep was not unusually low. However, after the chemoceptors also had been destroyed, blood pressure fell much lower during deep sleep. Analysis of variance, with multiple classification, shows that both differences are highly significant (p < .001).

These observations clearly indicate that the neural depressor influences active during deep sleep are effectively buffered in the intact animal by reflex chemoceptive discharge arising in the carotid bodies and, presumably, also in the aortic body. Recent data provided by electromagnetic flowmeters chronically implanted around the ascending aorta (4) suggest that chemoceptors may be stimulated during deep sleep because of stagnant anoxia resulting from decrease in cardiac output.

Our observations seem to suggest a normal physiological role for chemoceptors in circulatory homeostasis. While it is current opinion that these receptors are only an emergency mechanism, limited to such uncommon pathological events as acute anoxia or shock (5), our data suggest that their role includes entirely physiological conditions of everyday occurrence—like natural sleep—and that their physiological importance, as yet unknown as far as the normal unanesthetized animal is concerned (6), may be such as to avoid too-great falls in blood pressure and, at least in some animals, episodes of cerebral anoxia during deep sleep.

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"Sex-Ratio" Condition: Unusual Mechanisms in Bark Beetles

Abstract. *Although males and females occur in similar frequency in the broods of most scolytid beetles, certain individuals of several species produce offspring highly aberrant in the ratio of sexes—all or mostly female. In some instances this condition reflects gynogenesis (parthenogenesis stimulated by mating); in others, a maternally transmitted factor.*

Determination of sex in scolytid beetles is of the XX-XY type with homogametic females. The sex ratio of broods is usually about 1 : 1, but extreme departures may result from several different mechanisms. We have found individuals in two taxonomic groups that produce only or almost only female progeny. Two entirely different mechanisms are concerned: In *Orthotomicus* (formerly *Ips*) *latidens* a cytoplasmic factor is responsible, whereas in *Ips tridens*, *Ips englemanni*, *Ips simirosteris*, *Ips amiskwiensis*, and *Ips yohoensis* a type of parthenogenesis (gynogenesis) exists.

The phenomenon of "sex ratio" (SR) was first carefully analyzed by Gershenson (1) in *Drosophila obscura*, in which a particular X chromosome carried by a male results in production of all-female progeny. An apparently quite similar abnormality was earlier found in *D. affinis* (2), but the stock was lost before a detailed study could be made. Sturtevant and Dobzhansky (3) showed that the Y chromosomes degenerate regularly in SR strains of *D. pseudoobscura*. Novitiski *et al.* (4) found that, contrary to earlier reports, the X chromosomes behave normally. That the Y chromosomes show degeneration at second anaphase suggests that the SR condition can be interpreted in terms of regularly nonfunctional products of meiosis. Another type of mechanism, by which unisexual progeny have been produced in *Drosophila*, and which is

caused by cytoplasmic infections, also has been termed SR; these instances have been reviewed by Poulson (5) and covered by others (6). Poulson and Sakaguchi (7) found the infective agent to be a new species of *Treponema*-like spirochete, while a virus seems to be the agent in *D. bifasciata* (8). Lanier (9) reported a SR condition in *Orthotomicus latidens*.

We induced isolated pairs of beetles to produce brood by introducing them into small, freshly cut logs of their natural host; they were held separately in cardboard food cartons until the progeny were mature. All species deposit one egg in an individual niche on either side of a linear egg gallery in the phloem-cambial area of the tree. The larva makes a discrete mine beginning at the egg niche and terminating in a pupal chamber; thus, when the bark is stripped to recover the F_1 adults, the numbers of egg niches and larval mines are easily determined.

The SR line of *O. latidens* was collected in *Pinus jeffreyi* (10); its pedigree appears in Fig. 1. Three of the 11 females of the brood, paired with males of the same population, produced a total of 70 female and no male offspring. Some of the F_2 were paired with males of the same population and some with males from Lake County, about 480 km distant, without effect on the sex ratio of the progeny. Males sometimes appear in early broods of SR females, but subsequent broods from the same females usually contain only females (Fig. 1, F_3 generation). In the F_1 and F_2 generations (Fig. 1) approximately 50 percent of the egg niches yielded larvae; normally 92 percent of eggs produce larvae in the bisexual population. Some initial broods of the F_3 included a few males and had an overall larva : egg-niche ratio of 0.61, while second broods (females only) had a ratio of 0.49 (Fig. 1). The overall ratios in the F_4 generation were 0.47 for all-female broods and 0.82 for SR broods containing males. The male : female ratio for the latter broods was 0.65 : 1, which is almost exactly what we would have predicted from the larva:egg-niche ratio of 0.82 if the reduction in hatchability were attributable to mortality of male embryos (11). Unmated females fail to oviposit; those mated to the closely related species *O. sabinianae* oviposit but no eggs hatch (9).

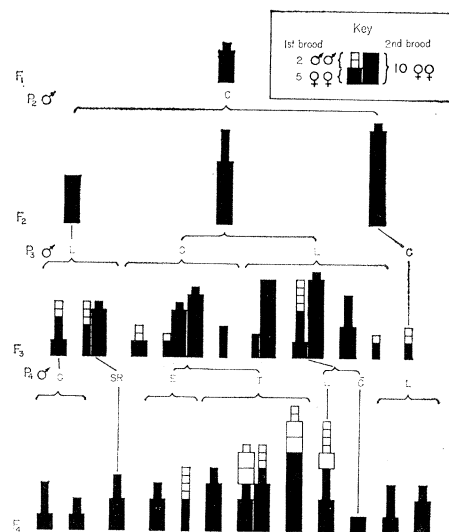The necessity for conspecific matings for progeny, and the very close

Fig. 1. SR line of *Orthotomicus latidens*, F_1 through F_4. A small square represents one individual; a large square, five. Black, female; white, male. Contiguous histograms sequentially arranged from left to right represent successive broods by the same female (see key). Parent females were from broods indicated by brackets. The parent males came from these Californian counties: Calaveras (C) (source of the SR strain), Lake (L), El Dorado (E), and Tahoe (T); SR, from SR brood.

correlation between egg hatchability and number of males in SR broods, indicate that SR condition in *O. latidens* reflects mortality of the male embryos. The uniform inheritance of the condition through several generations of random and selected matings and the matrilineal nature of the inheritance suggest that male mortality cannot be caused by sex-linked or sex-limited genes per se; rather it must be a factor transmitted in the cytoplasm of the egg. All our results with this species parallel the instances of infected *Drosophila* previously mentioned. Unfortunately attempts to identify an agent from the hemolymph of *O. latidens* with phase-contrast and darkfield microscopy have failed; failure suggests that the causative agent may be a virus rather than a spirochete unless either its distribution in the host is limited or the titers are very low.

Hopping (12) discovered SR strains of four Canadian bark beetles, *Ips tridens*, *Ips englemanni*, *Ips simirosteris*, and *Ips amiskwiensis*; in four generations there was no change in all-female broods and apparently no reduction in number of progeny. Smith (13), examining Hopping's data, suggested that the females might be gynogenic. We can now confirm that in-