pocampal and lateral septal unit activity increases progressively over training for conditioning animals only, medial septal neuronal responses decrease across trials for both paired and unpaired groups (Table 1). For both the lateral septal and medial septal responses, a 2 × 13 analysis of variance was computed for paired versus unpaired standard score measures over all blocks of trials. Consistent with the interpretation of medial septal activity as sensory evoked responses, analysis of variance failed to reveal any significant differences between groups in paired and unpaired conditions for either period, on either day. Moreover, responses during both paired and unpaired CS periods ($P < .05$) and UCS periods ($P < .01$) showed a significant across-block decrement on day 1. Lateral septal trends were also confirmed, with the between-groups effect significant for the UCS period on both days ($P < .01$, day 1; $P < .05$, day 2), and the CS period differences reaching significance ($P < .05$) by day 2.

Although many studies have indicated septal involvement in learning (*2*), our findings now argue for a distinction between possible roles of the medial and lateral septal nuclei. Neuronal records obtained from the lateral septum are completely consistent with anatomical descriptions of that area as a primary efferent projection site for hippocampal pyramidal cells (*1*). These results further support an association between hippocampal function and learned behavior (*3*), as most aspects of hippocampal cellular response correlated with nictitating membrane conditioning are also seen at the level of the lateral septum. On the other hand, our findings imply that the medial septum may function in an afferent capacity with respect to the hippocampus, at least in this learning paradigm, responding primarily to stimulus onsets. This implication is supported by anatomical evidence (*1*) and is in accordance with characterizations of medial septal activity as "arousal" in nature (*5*).

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Event-Related Brain Potentials: Comparison Between Children and Adults

Abstract. *Event-related brain potentials in response to tachistoscopically presented stimuli were recorded from adults and children. Rare, nontarget stimuli (both novel and easily recognized) elicited different brain potentials in children and adults, while equally rare, target stimuli elicited similar potentials in children and adults.*

Although the averaged event-related brain potential (ERP) has been studied in infants and children (*1*), ERP wave forms with latencies later than 250 to 300 msec have seldom been examined. Shelburne (*2*), studying children aged 8 to 12 years found late positive waves (latency, 450 to 600 msec) in response to the last letter of three-letter words that were presented one letter at a time, tachistoscopically. Symmes and Eisengart (*3*), however, studying children aged 5 to 11 years, found large negative waves (latency, 520 msec) in response to colorful pictures of cartoon figures and familiar objects such as toothbrushes and keys; they did not report finding P3 waves or any other late positive waves. It is unclear whether the different waves found in these two studies reflect differences in subject populations, tasks, stimuli, or attention or arousal levels. Furthermore, no comparisons of such late waves in children with those in adults have been reported.

In an effort to compare late waves elicited in normal children to those of adults, I presented four categories of visual stimuli to ten children (age 6 to 8 years) and ten adults (age 23 to 35 years) (*4*). The results show that novel and easily recognized stimuli that are nontargets (that is, not counted by the subject) and deviate from an ongoing sequence of background stimuli elicit very long latency negative and positive waves in children (termed Nc and Pc waves); in contrast, such stimuli consistently elicit P3 waves in adults. However, in response to equally infrequently presented but target stimuli (those counted by the subject), P3 waves similar to those seen in adults are recorded in children.

Each subject reclined in an easy chair 2.5 m from a viewing screen. Slides were flashed onto this screen at regular intervals of 1250 msec; each flash lasted 80 msec and subtended 2.3° of visual angle. Subjects fixated their eyes on a dot at the center of the viewing screen during slide presentations.

Four types of visual stimuli were used in different phases of this experiment: (i) slides bearing the letter A, each subtending a visual angle of 0.5° and having a luminance of 1.8 log cd/m^2; (ii) slides bearing the letter B with the same visual angle and luminance as A slides; (iii) slides bearing any letter from C to Z, each subtending a visual angle of 0.2° and having a luminance of 1.3 log cd/m^2 (termed dim); and (iv) slides bearing novel stimuli, each consisting of a different, quasi-random, unrecognizable color pattern, subtending a visual angle of 2.3° and having a luminance of 1.2 log cd/m^2 (*5*).

Before the recording session began, each subject was shown a sample 20-slide sequence of A's and B's and was told that the slides would be presented in blocks of 50 with a 1-minute rest period between blocks (*6*). The subjects were instructed to relax, to keep a running count in their heads of the number of targets in each block, and to disregard all other stimuli. At the end of each block, they were to report this count to the experimenter.

Each subject was exposed to three experimental conditions. For half of the subjects in each age group, in the first two conditions the B's were the background (nontarget) stimuli to be ignored and the A's were the targets to be counted; in the third condition, the A's were the background stimuli and the B's were targets. For the other half of subjects, the target and nontarget stimuli were reversed in each condition. In the first condition, only one block of slides consisting of 88 percent background stimuli and 12 percent targets was presented. The second and third conditions each contained three blocks of slides, each block consisting of 76 percent background slides and 12 percent targets; the remaining 12 percent were either novel or dim slides (*7*). For half of the subjects in each age group, novel slides were presented in the second condition with the dim slides in the third; the reverse was true for the other half. Slides were randomly mixed within each block. Each novel or dim slide was presented no more than once to a given subject.

Beckman nonpolarizable electrodes were placed at Fz, Cz, and Pz, as specified in the 10-20 system; each was referred to the right mastoid process. Electrooculograms (EOG's) were recorded with Beckman electrodes placed above and below one eye so as to detect eye blinks as well as vertical and lateral eye movements (*8*). Each eye lead was also separately referred to the right mastoid process (*9*).

Electroencephalograms (EEG's) were recorded with a Grass Model 7 polygraph with 7P5 a-c preamplifiers (bandpass down 3 db at 0.15 and 500 cycle/sec). For all subjects, the EEG output was stored on FM magnetic tape. The EEG was also written out on paper for visual inspection; all trials with eye blinks, eye movements, or excessive muscle artifact were excluded from subsequent averaging and analysis (*10*). The ERP's for each of the stimulus categories were averaged with a Fabritek 1052 signal averager (*11*).

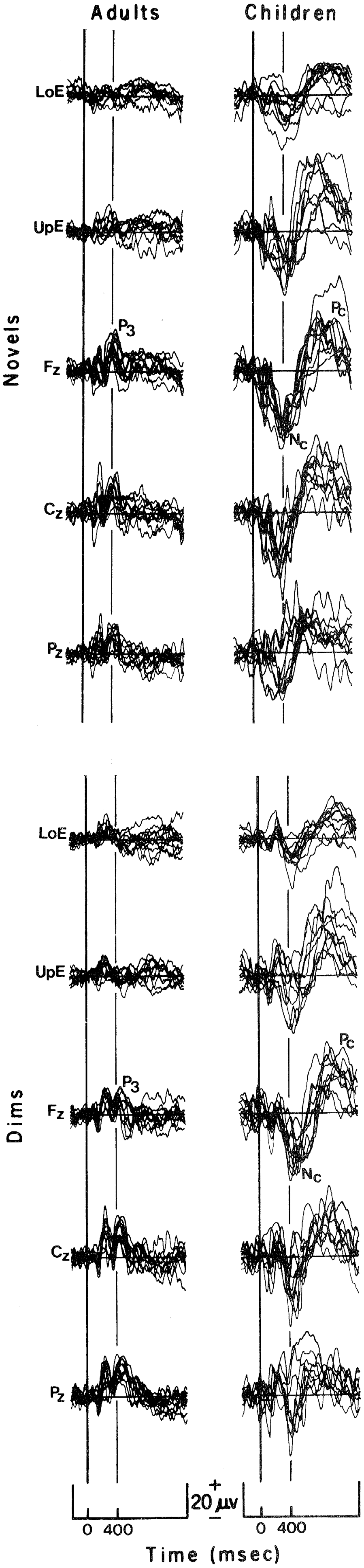

Fig. 1. Averaged ERP's elicited by novel and dim slides from each of ten children and ten adults. Each trace represents an average of 16 responses from one child or of eight responses from one adult; *LoE*, lower eye lead referred to mastoid; *UpE*, upper eye lead referred to mastoid.

All four categories of stimuli elicited N1-P2 waveforms in children as well as in adults (Figs. 1 and 2). Overall, these waves do not show substantial differences between age groups in either latency or amplitude at Cz (*12*). However, the waves later than P2 elicited by dim and novel slides showed significant differences between children and adults. The ERP's from each subject are shown, superimposed, in Fig. 1. In every child tested, both novel and dim slides elicited very high amplitude, frontally distributed, negative waves (Nc) (at Fz, 33.4 μv and 394 msec for novel slides; 27.8 μv and 504 msec for dim slides), and positive waves (Pc) (at the upper eye, 31.5 μv and 967 msec for novel slides; 34.6 μv and 982 msec for dim slides) (*13*); these large Nc waves were not seen in any of the adults tested. The novel stimuli elicited significantly higher-amplitude and shorter-latency Nc waves than did the dim slides (*13*). No significant differences were found in the scalp distribution of Nc waves for novel and dim slides, nor were there differences in the scalp distribution of Pc waves for novel and dim slides. However, Pc waves were significantly more frontally distributed than Nc waves [for scalp locus–stimulus type interaction, $F(4,32) = 4.88$ for dim slides ($P < .005$) and 2.85 for novel slides ($P < .05$)]; Pc waves were largest at the upper eye site while Nc waves were largest at Fz.

Electroocular activity may be dismissed as the source of these Nc and Pc waves for the following reasons. The data of Overton and Shagass (*14*) indicate that eye blinks and vertical eye movements produce electrical potentials of opposite polarities above and below the eye. In four children and two adults, I found that vertical eye movements and eye blinks produce potentials of opposite polarities in the upper and lower eye derivations, in agreement with Overton and Shagass. In the current study, Nc and Pc waves at electrode sites above and below the eye were of the same polarity and therefore cannot be caused by eye blinks or vertical eye movements. Furthermore, Overton and Shagass (*14*) showed that potentials derived from EOG activity are maximal around the eye; the Nc wave in the present study had maximal amplitude at Fz, with amplitude at the upper eye derivation being only 67 percent of this for novel slides and 50 percent for dim slides and those at the lower eye derivation only 35 and 45 percent, respectively (*15*).

These waves are also unlikely to be

electroretinogram (ERG) potentials because the amplitude distributions of Nc and Pc waves around the eye are different from those reported by Noonan *et al.* (*16*) for *a* and *b* waves of the ERG. The Nc waves had maximum amplitude at Fz and were larger above the eye than below; Pc waves had maximum amplitude above the eye, with amplitude at Fz being 83 percent of this for novel slides and 81 percent for dim slides. However, the lower eye amplitude was only 37 percent of that for the upper eye for novel slides and 38 percent for dim slides. Noonan *et al.* (*16*) showed that for several directions of gaze (central gaze and 35° lateral, medial, upward, and downward from central gaze), the amplitudes of *a* and *b* waves at infraorbital derivations were much larger than amplitudes recorded above the eyebrow (except for 35° upward gaze, in which the amplitudes were nearly equal). Thus, whereas Nc and Pc waves are larger above the eye than below, *a* and *b* waves are larger below than above. Also, Nc and Pc waves have latencies of several hundred milliseconds, while those of *a* and *b* waves are generally less than 100 msec (*16, 17*).

Novel and dim slides elicited P3 waves instead of long-latency Nc waves in every adult tested (Fig. 1) (*18*). In agreement with recent studies on adults (*6*), easily recognized, nontarget stimuli that were infrequently presented (dim slides) elicited posteriorly distributed P3 waves, while unrecognizable, novel stimuli (novel slides) elicited centrofrontally distributed P3 waves. The scalp distributions of these two types of P3 waves differed significantly [for scalp locus–stimulus type interaction, $F(2,18) = 28.9$, $P << .00001$].

The scalp distribution of P3 waves in adults was significantly different from that of Pc waves elicited by novel and dim slides in children [P3 compared to Pc, scalp locus–wave type interaction: $F(4, 64) = 10.1$ ($P << .001$) for novel slides and 9.95 ($P << .001$) for dim slides]. These distribution differences could reflect any one of several possibilities: (i) each of these late positive waves could have different brain generators; (ii) the same brain generator (or generators) could underlie all of these positive waves, with distribution differences due to age-related differences in generator geometry; or (iii) the same brain generator (or generators) could underlie all of these positive waves, with distribution differences due to age-related differences in the time of initiation, the intensity, or the time course of generator activity.

Both target and background stimuli elicited posteriorly distributed P3 waves in adults and children (*19*); ERP's for target stimuli at Pz from each child and adult tested are shown in Fig. 2. There were no substantial differences between adults and children in the scalp distribution or amplitudes of P3 waves for target or background stimuli (*20*). However, the target P3 waves had significantly longer latencies in children than in adults [at Pz, mean latency of 702 msec for children (range, 502 to 966 msec) and 417 msec for adults (range, 380 to 461 msec); $t = 5.79$, $P < .00001$]. I found no corresponding differences between adults and children in the latencies of N1 or P2 waves elicited by targets. In all 20 subjects, the amplitudes of target P3 waves at Pz were greater than those of background P3 waves. Thus, although rare, nontarget stimuli elicit different ERP's in children and adults, rare stimuli to which an explicit external importance has been established (target stimuli) elicit similar P3 responses in both children and adults.

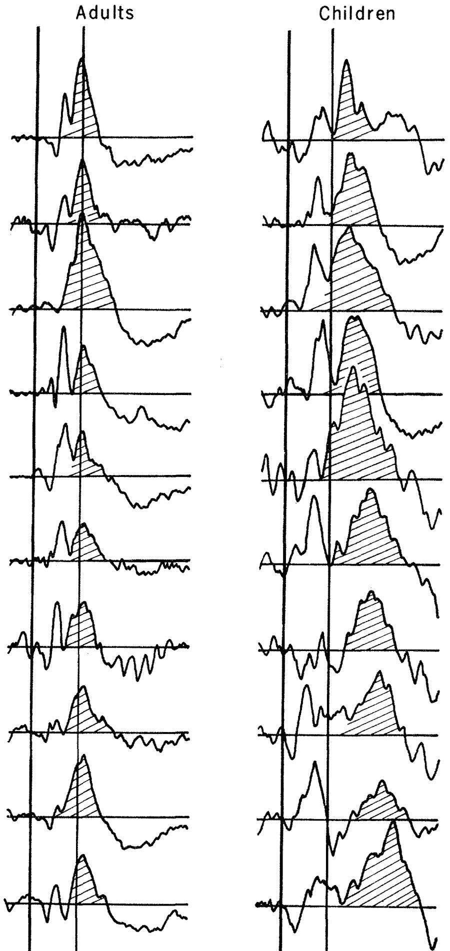

Fig. 2. Averaged ERP's for target stimuli at Pz from ten adults and ten children. Each trace represents an average of 32 responses from one subject. P3 waves are stippled. The ages (in years) and genders of the children whose ERP's are shown (top to bottom) are 7.0 ♂, 7.8 ♀, 7.4 ♀, 7.8 ♀, 6.5 ♂, 7.0 ♀, 7.7 ♂, 7.4 ♀, 6.0 ♂, and 6.8 ♂.

In conclusion, while nontarget stimuli (novel or easily recognized) that are infrequently presented and deviate from the background elicit P3 waves in adults, such stimuli elicit Nc and Pc waves in children. Also, while the scalp distribution of P3 waves in adults seems to vary with the ease of stimulus recognition or the degree of stimulus novelty, the Nc and Pc distributions in children do not seem to vary with these factors. These differences between children and adults in ERP's suggest corresponding differences in the mode of processing employed by each group when rare, deviant stimuli (novel and dim slides) were encountered (*21*). In contrast, children and adults appear to process rare, target stimuli in a similar fashion, as indicated by target P3 waves; the differences between adults and children in the P3 latencies for targets suggest corresponding differences in speed rather than mode of processing (*22*).

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4. The adult and children's groups each consisted of five females and five males. (Two additional children were tested, but all of their data were excluded because of excessive eye blinking.) For all of the children and eight adults, this was their first experience in an ERP experiment; two adults had been subjects in auditory ERP experiments.
5. These stimulus categories are the same as those used in previous studies on adults in which I distinguished three types of late waves elicited by infrequently presented stimuli: (i) a P3 wave largest over centrofrontal scalp sites elicited by unrecognizable, novel stimuli; (ii) a P3 wave largest over parietal scalp sites elicited by nontarget, easily recognized stimuli; and (iii) another P3 wave largest over parietal scalp sites elicited by target stimuli [E. Courchesne, S. A. Hillyard, R. Galambos, *Electroencephalogr. Clin. Neurophysiol.* **39**, 131 (1975); E. Courchesne, R. Courchesne, S. A. Hillyard, in preparation]. These results suggest that such stimulus categories could prove to elicit an equally interesting array of late waves in children.
6. No subject knew that infrequent, nontarget stimuli would be presented; subjects were told that the purpose of the experiment was to examine how brain responses change with age.
7. Before each block, subjects were instructed to pay attention only to the target stimuli and to ignore all other stimuli.
8. One electrode was placed just below the in-

fraorbital ridge and 1 cm medial to a line bisecting the pupil in central gaze. The other electrode was placed just above the eyebrow and 1 cm lateral to a line bisecting the pupil in central gaze.

9. The skin under each electrode was abraded and was punctured with a sterile needle at Fz, Cz, Pz, and the right mastoid. Electrode impedences were never greater than 2000 ohms for Fz, Cz, and Pz and 5000 ohms for the upper and lower eye leads.
10. In each stimulus category, only an average of 4 and 12 percent of trials were excluded for these reasons for adult and children's groups, respectively.
11. The ERP wave forms were measured either peak to peak or baseline to peak with 250 msec of the average prestimulus EEG tracing serving as baseline.
12. The mean N1-P2 amplitudes at Cz in children were 25.2 μv for targets, 21.2 μv for background slides, 18.5 μv for novel slides, and 19.9 μv for dim slides. The mean N1-P2 amplitudes at Cz in adults were 21.1 μv for targets, 16.1 μv for background slides, 13.7 μv for novel slides, and 22.2 μv for dim slides. The mean N1 and P2 latencies at Cz in children were 144 and 259 msec for targets, 148 and 238 msec for background slides, 173 and 243 msec for novel slides, and 155 and 266 msec for dim slides. The mean N1 and P2 latencies at Cz in adults were 150 and 240 msec for targets, 152 and 243 msec for background slides, 133 and 209 msec for novel slides, and 158 and 246 msec for dim slides.
13. The mean amplitudes of Nc waves in children for novel slides were 11.6 μv at the lower eye (LoE), 22.3 μv at the upper eye (UpE), 33.4 μv at Fz, 29.9 μv at Cz, and 19.0 μv at Pz; the mean amplitudes of Nc waves in children for dim slides were 12.5 μv at LoE, 14.0 μv at UpE, 27.8 μv at Fz, 23.0 μv at Cz, and 15.1 μv at Pz. The mean amplitudes of Pc waves in children for novel slides were 11.6 μv at LoE, 31.5 μv at UpE, 26.2 μv at Fz, 25.6 μv at Cz, and 14.4 μv at Pz; the mean amplitudes of Pc waves in children for dim slides were 13.0 μv at LoE, 34.6 μv at UpE, 28.0 μv at Fz, 21.9 μv at Cz, and 11.8 μv at Pz. [In a few children, P3-like waves (latency of about 650 msec) were seen at Pz in response to novel and dim slides (five of ten subjects in each case)]. A comparison of amplitudes of Nc waves for novel and dim slides at Fz gave $t = 2.60$, $P < .03$ (two-tailed test); a comparison of latencies at Fz gave $t = 2.88$, $P < .02$ (two-tailed test).
14. D. A. Overton and C. Shagass, *Electroencephalogr. Clin. Neurophysiol.* **27**, 544 (1969).
15. Lateral eye movements may be discounted as the source of the Nc and Pc waves for the same reasons. Movements to the right produced positive potentials in the upper eye lead and negative ones in the lower eye lead. The opposite was true for movements to the left. Also these eye movement potentials were largest in the upper eye lead with Fz, Cz, and Pz derivations having successively smaller potentials.
16. B. D. Noonan, R. J. Wilkus, G. E. Chatrian, E. Lettich, *Electroencephalogr. Clin. Neurophysiol.* **35**, 495 (1973).
17. T. P. Fogarty and R. N. Reuben, *Arch. Ophthalmol.* **81**, 454 (19 → A. Lodge, J. C. Armington, A. B. Barnet, B. L. Shanks, C. N. Newcomb, *Child Dev.* **40**, 267 (1969).
18. The mean P3 amplitudes in adults for novel slides were 1.5 μv at LoE, 5.5 μv at UpE, 15.2 μv at Fz, 15.5 μv at Cz, and 12.7 μv at Pz; the mean P3 amplitudes in adults for dim slides were 0.0 μv at LoE, 0.9 μv at UpE, 11.4 μv at Fz, 17.2 μv at Cz, and 17.5 μv at Pz. The mean P3 latencies at Cz were 411 and 448 msec for novel and dim slides, respectively.
19. The mean target P3 amplitudes were 9.6 μv at Fz, 24.0 μv at Cz, and 28.6 μv at Pz for children; and 11.0 μv at Fz, 18.4 μv at Cz, and 19.5 μv at Pz for adults. The mean P3 amplitudes for background stimuli were 5.3 μv at Fz, 9.9 μv at Cz, and 9.1 μv at Pz for children; and 4.4 μv at Fz, 7.0 μv at Cz, and 8.1 μv at Pz for adults.
20. A comparison of the mean amplitudes of target P3 waves at Pz for adults and children gave $t = 203$, $P > .06$ (two-tailed test). Comparisons of the distribution of P3 waves to background and target stimuli for adults and children each yielded $P > .50$.
21. This does not suggest that all paradigms using such deviant stimuli will produce such differences or that P3 waves to these stimuli are never found in children.
22. Adults made less than 1 percent errors in target counts and the children made only 2 percent errors. Both groups used similar methods to keep count (such as repeating to oneself the current count each time a stimulus flashed and incrementing this count each time a target flashed). Also, subjects in each age group stated that they were surprised when they saw the first dim or novel slide. However, unlike the adults, most children attempted to label or identify (often in idiosyncratic ways) the novel slides by using concrete constructs (for example, "one slide looked like a horse," or "was there one with a house and flowers?").
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Two Genes Control Seasonal Isolation in Sibling Species

Abstract. Interspecific hybridization tests between Chrysopa carnea *and* Chrysopa downesi *show that single allele differences at two unlinked autosomal loci cause large differences in photoperiodic responses. These differences produce asynchronous seasonal reproductive cycles, thus forming an effective temporal reproductive barrier between the two sympatric species. The results subserve the development of a genetic model for allochronic speciation.*

Evolutionary biologists generally imply or state directly that a prerequisite for sympatric speciation in bisexual animals is the attainment of a high degree of reproductive isolation through very simple genetic changes (*1*, *2*). However, there are very few proposed cases of sympatric speciation in which this requirement is shown to be fulfilled, and all of these cases deal with speciation in monophagous or parasitic animals through host race formation (*2*). For example, in monophagous tephritid flies alteration of a single allele can produce a shift in host plant preference (*3*). Such a change sets the stage for sympatric speciation because these insects generally mate on the preferred host, and a single allele difference at the locus controlling host selection can thus confer a substantial amount of reproductive isolation between host races (*4*). Similar mechanisms of sympatric speciation through host race formation have been proposed for other monophagous insect species (*5*). In comparison to these examples, proposed cases of sympatric speciation through seasonal isolation (that is, allochronic speciation) are not as well supported either experimentally or theoretically; and these deficiencies have contributed appreciably to the controversy of whether or not seasonal isolation is indeed a mechanism of speciation (*6*). Specifically, the primary impediment to the development of an acceptable model (or models) for allochronic speciation is the lack of the necessary experimental evidence that a simple genetic change can produce a functional asynchrony in the seasonal occurrence or cycles of reproduction in animals (*7*). In fact, there exists considerable evidence to the contrary; numerous studies have illustrated that polygenes or complex genetic mechanisms underlie interracial and interspecific differences in seasonality (*8*). Our recent experiments with interspecific hybrids indicate that gross differences in the seasonal reproductive cycles between two sympatric species result from single allele differences at each of two autosomal loci. These small genetic differences produce an asynchrony in the species' seasonal patterns of reproduction that is sufficient to provide a high degree of reproductive isolation. Thus, our findings provide a basis for developing a realistic

Table 1. Diapause characteristics of F_1 progeny from hybrid and conspecific crosses of *C. carnea* and *C. downesi*, reared under LD 16:8 at 24° ± 1°C. The numbers in parentheses indicate the number of animals.

F^1 progeny*	Percent diapause	
	Male	Female
d–c	0 (31)	0 (33)
c–d	0 (33)	0 (32)
c–c	0 (25)	0 (25)
d–d	100 (25)	100 (24)

*d, *C. downesi*; c, *C. carnea*; female parent indicated first.

Table 2. Diapause characteristics of progeny from F_1 hybrid × F_1 hybrid crosses, reciprocal F_1 hybrid × *C. downesi* backcrosses, and conspecific pairings (LD 16:8, 24° ± 1°C). The numbers in parentheses indicate the number of animals.

Progeny*	Percent diapause
F_1 hybrid × F_1 hybrid	
dc–dc	5.2 (96)
cd–cd	8.6 (70)
Backcrosses	
dc–dd	25.0 (52)
cd–dd	36.5 (52)
dd–dc	15.6 (45)
dd–cd	21.2 (52)
Conspecific	
dd–dd	100.0 (27)
cc–cc	0.0 (36)

*d, *C. downesi*; c, *C. carnea*; female parent indicated first.