class than in the nonmanual. These variations presumably reflect population changes in childbearing patterns.

The first proposition was tested in the brothers series. This proposition suggests that the difference score (firstborn score minus secondborn score) should be negatively related to spacing. As is apparent in Fig. 1A, in a simple linear regression the association is not different from zero (*10*).

The second proposition was tested in the brothers series and the population series. It suggests that there should be a positive relation between spacing interval and the ability scores of the firstborn and of the secondborn in both series and also the average ability scores of brother pairs ("average ability score" was used to retain the paired status of brothers within given intervals). None of the relationships were statistically significant, in either the brothers series or the population series (*10*). This is shown for ability score in the brothers series in Fig. 1B.

Thus neither proposition was upheld. Increased spacing was not an advantage for secondborn (brothers series) nor was it systematically related to improved ability among brothers or in firstborn and secondborn individuals (population series).

There was a positive association between mother's age at the birth of the first child and ability. On the other hand, there was a negative association between mother's age and spacing in that among older mothers the interval between the two children tended to be shorter. Maternal age therefore could have suppressed the effects of spacing. To test this possibility, a multiple-regression analysis (*11*) was done for the two series. In the brothers series, the two dependent variables, average ability level and difference score, were used. The independent variables were mother's age, mother's age squared, interval, and interval squared. There was a statistically significant relation between average ability and mother's age and mother's age squared, accounting for between 5 and 10 percent of the variance. Average ability was not related either to interval or interval squared. Difference score was related neither to mother's age nor to interval.

In the population series, too, the relation of ability score to mother's age and mother's age squared was statistically significant and accounted for about 3 percent of the variance. Ability score was not related to interval or to interval squared.

We conclude that in two-child families the interval between the children does not explain the birth-order effect on their adult intelligence. It remains possible that the spacing of births could contribute to such advantage in larger families.

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8. The military supplied us with names for the military registration numbers we selected from our original data set; this information was forwarded to the Amsterdam registrar, who searched the local population register for the year of birth of the individual's mother, the birthdate and sex of his sibling, and, for a male sibling, his military ID number if available. (There are no further data for sisters.) This information was made anonymous again before being sent to us. As a second step, we obtained photocopies of the actual military examination records of all young men for whom we had information on spacing interval and maternal age. From these we abstracted the raw scores on the five tests administered as part of the preinduction procedure (Bennett Test of Mechanical Comprehension, Raven Progressive Matrices—Dutch modification, and tests of arithmetic, language and grammar, and clerical aptitude). The Dutch rated raw scores on a scale of 1 to 6. We applied the same rating standard to all raw scores of those in the brothers series. Intercorrelations among the tests ranged from .348 to .732 [F. A. Marolla, thesis, New School for Social Research, New York (1973)]. Correlations of the individual tests with total score ranged from .647 to .853.
9. M. Susser, *Causal Thinking in the Health Sciences* (Oxford Univ. Press, New York, 1973).
10. Correlations with spacing were as follows. For statistical significance, all correlations, except for difference score, should be positive in sign.

	r	*t*	d.f.
Brother series			
Difference score			
Manual	.07	1.01	226
Nonmanual	−.01	−.13	305
Average ability			
Manual	−.12	−1.89	226
Nonmanual	−.01	−.26	305
Firstborn ability			
Manual	−.14	−2.10	226
Nonmanual	−.01	−.17	305
Secondborn ability			
Manual	−.07	−1.08	226
Nonmanual	−.02	−.28	305
Population series			
Firstborn ability			
Manual	.03	.48	337
Nonmanual	−.07	−1.35	399
Secondborn ability			
Manual	.03	.64	349
Nonmanual	−.01	−.29	418

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Long-Latency "Subthreshold" Collicular Responses to the Constant-Frequency Components Emitted by a Bat

Abstract. *A previously undescribed response pattern has been observed in certain single units in the posterior colliculus of* Pteronotus suapurensis. *These units, constituting about one-third of those tuned to the region of the dominant constant-frequency (CF) components of the orientation sounds, respond to a tone pip with a burst of spikes at a latency of 3 to 6 milliseconds, within the frequency-intensity domain of a normal V-shaped response area. In these units, however, as intensity is dropped below threshold for this response, a response of 5- to 10-milliseconds longer latency appears and persists throughout another 10 to 30 decibels of attenuation. These late responses can be very vigorous, are sharply tuned to frequencies at or just above the CF components of the signal, and are often strongest and of lowest threshold at stimulus durations of 1.5 to 3 milliseconds—approximately the duration of the CF component. These properties imply that the late responses are concerned with analysis of the CF components of echoes, apparently in ways not as prominent in other bats.*

Different species of bats emit different types of echolocation sounds and exhibit auditory specializations appropriate for the signals used (*1*). It is of special interest to examine auditory adaptations in two species of the same genus that use very different orientation sounds. The Neotropical genus *Pteronotus* offers such an opportunity. *Pteronotus parnellii* emits 15- to 25-msec constant-frequency (CF) pulses with a dominant component of approximately 61 to 62 kHz, terminating in a 1- to 2-msec sweep to about 55 kHz. From the level of the cochlea (*2*)

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and posterior colliculus (*3*) to the auditory cortex (*4*), this species shows overwhelming emphasis on accurate frequency resolution in the range 60 to 63 kHz. This capability allows the bat to make use of the Doppler-shift information in echoes (*5*). Evoked potentials in *P. parnellii* show relatively slow recovery of responsiveness following a stimulus (*3*), compared with the very rapid recovery of responsiveness in bats emitting purely frequency-modulated (FM) signals (*6*). A smaller species of the same genus, *P. suapurensis*, emits pulses consisting of a 2- to 3-msec CF component of approximately 52 kHz (with a prominent harmonic at approximately 78 kHz), ending in an FM sweep to about 42 kHz. This species is broadly tuned throughout the frequency range of the emitted orientation sounds, with little evidence of peripheral specialization for accurate frequency resolution around 52 kHz (*3*). Also, this species exhibits phenomenally fast recovery of evoked potential responsiveness, with dramatic short-term facilitation of response to the second of two signals of the same frequency, even one 30 to 50 dB fainter than the first (*3*). Recovery of evoked potential responsiveness to the second of two stimuli is more remarkable in *P. suapurensis* than in any other species studied to date.

Because of this extreme adaptation for fast recovery, but lack of apparent specialization for use of the brief CF component, we have investigated the response properties of single units of this species, mostly in the posterior colliculus (*7*). In the course of this research a new type of single-unit response behavior was observed, to the best of our knowledge unlike any reported previously in bats or other animals. This behavior indicates the existence of a new form of auditory analysis, dealing with information contained in the brief CF component of the echoes in this species.

Figure 1A shows characteristic tuning curves of such units. Units of this type tended to have narrow response areas. Within this area, as the stimulus intensity was decreased, the firing rate fell and the probability of response decreased until, eventually, thresholds were reached describing the typical "response area" curves of Fig. 1 (a_1, b_1, and c_1). However, in this new class of units, as the stimulus was further attenuated the units again began to show a response but at 5 to 10 msec greater latency (Fig. 2A). Often this late response was more vigorous than the shorter latency response at any intensity. The late response then persisted through another 5 to 30 dB of attenuation (Fig. 1, curves a_2, b_2, and c_2). Occasionally a single unit showed both early and late responses at intensities near threshold for the early response, although there was seldom more than 2 or 3 dB of overlap of the response areas. Of 75 single units studied in seven *P. suapurensis*, 23 showed such a late response, with the minimum threshold of the late response ranging from 3 to 35 dB lower than the early response (mean ± standard deviation, 14.4 ± 7.8 dB). The early response occurred typically at a minimum latency of 3 to 6 msec; the late response had a minimum latency of 12 to 18 msec. This behavior was not seen in units more peripheral than the posterior colliculus, but a systematic study of other nuclei was not done.

All of these late responses were found in units tuned to one of two frequency bands: 53 to 58 kHz and 68 to 80 kHz. The vast majority were centered at 54 to 56 kHz, at or slightly above the dominant CF of the emitted orientation sounds. The 68- to 80-kHz band in which late responses were seen corresponds approximately to the next higher CF harmonic in the emitted pulses. In most cases, the best frequency for the late response corresponded closely to that of the early response in the same unit. However, there was sometimes a difference of 5 to 10 kHz, with the best frequency of the early response either at higher or lower frequencies. The late responses were normally more narrowly restricted than the early responses in the band of frequencies that could elicit a response.

Even within the two frequency ranges where late responses were found, a majority of units studied did not show the late response. During different microelectrode penetrations of the colliculus, clusters of units showing late responses were found in some locations, not in others; but no consistent pattern of distribution was found. Where late-responding units were found, however, nests of units were seen showing similar behavior, and the electrode recorded a late negative evoked potential that also appeared only at low intensities. This late slow wave was often larger than the earlier negative slow wave at any intensity within 40 to 60 dB above threshold. Figure 2 shows localized negative evoked potentials, with single units superim-

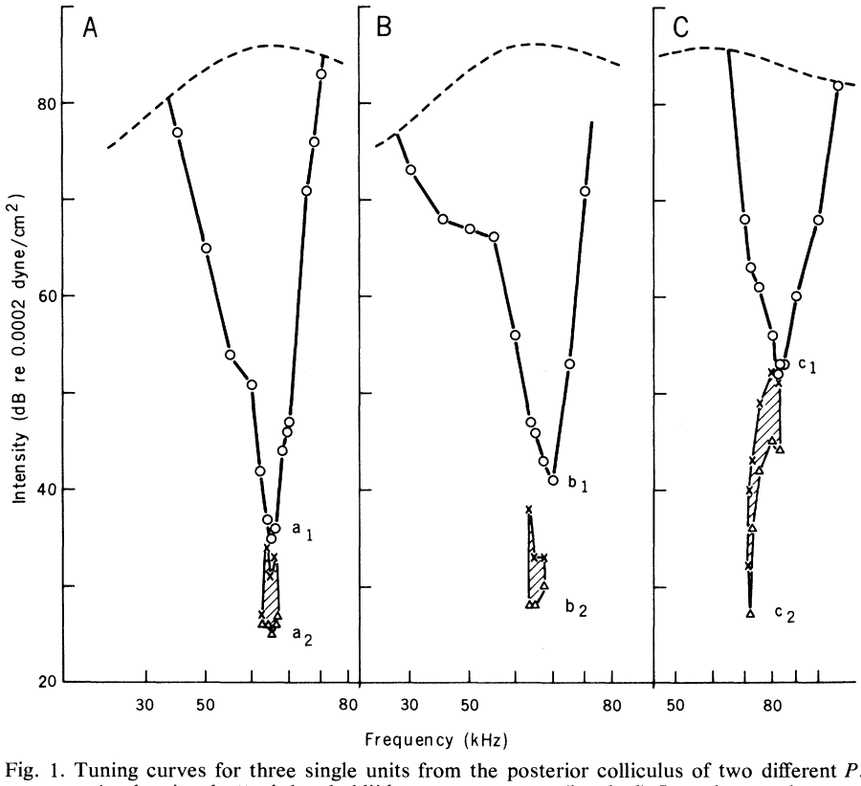

Fig. 1. Tuning curves for three single units from the posterior colliculus of two different *P. suapurensis*, showing the "subthreshold" late response areas (hatched). In each case, the upper (solid line) response area (a_1, b_1, and c_1) was determined by measuring at each frequency the lowest intensity at which the signal evoked one or more spikes from the unit at least 30 percent of the time, at the short latency normally associated with collicular units (3 to 6 msec). As the stimulus was attenuated further, the same units showed vigorous long-latency (12 to 18 msec) responses within the frequency-intensity domain indicated by the hatched areas (a_2, b_2, and c_2). For the late responses, the low-intensity threshold at each frequency is denoted by a △, the high-intensity threshold by an X. The dashed line at the top of each graph indicates the maximum signal intensity available.

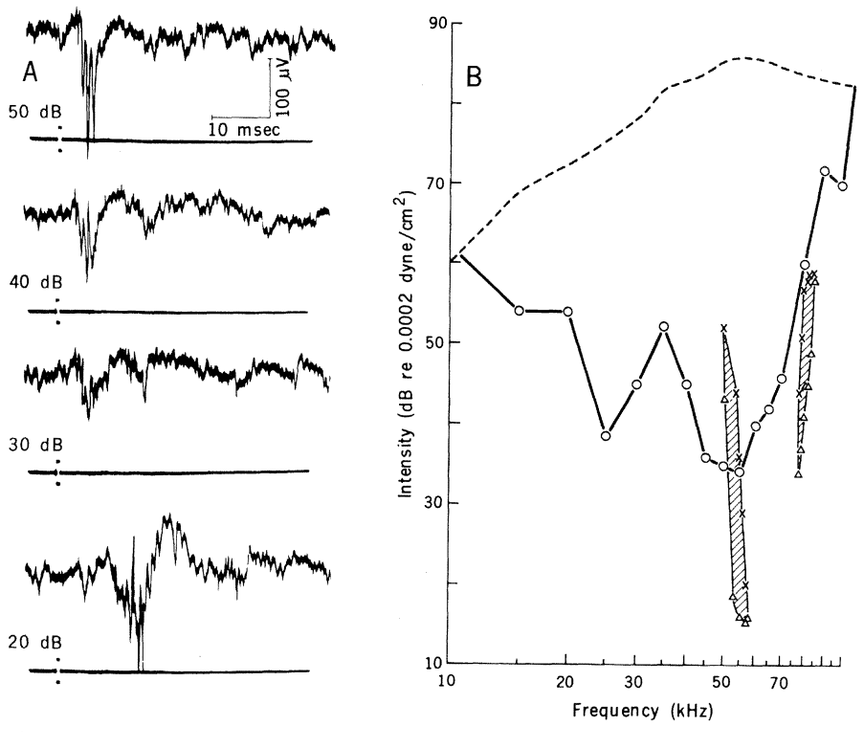

Fig. 2. (A) Characteristic oscilloscope traces, recorded with an etched tungsten microelectrode, showing the evoked potential responses near the electrode tip, with single units riding on the slow waves. Two or three large single units were present in several of the traces. These were probably the same units in all cases, but they could not be individually identified in this case. The stimulating frequency was 56 kHz and the intensity was as shown. As the intensity was decreased in 10-dB steps, the short-latency response decreased, the large single units dropped out, a small longer latency evoked response appeared, and at an intensity at which the early response had almost disappeared, the late response suddenly became very prominent with large single units again present. (B) Evoked potential "audiograms" for the short-latency slow-wave response at a given microelectrode location in the posterior colliculus and the response areas for the long-latency response (hatched) recorded at the same location. Note that the late responses were found in two narrow frequency ranges, corresponding approximately to the principal CF frequencies of the orientation sounds of *P. suapurensis*.

posed, at four different intensities (Fig. 2A) and a graph of the evoked potential audiograms of "early" and "late" responses at one location (Fig. 2B). These sensitive late responses were not "off-responses," such as have been described for *P. parnellii* and, less prominently, for *P. suapurensis* (*3*). The late responses occurred at the same time, independent of stimulus duration, even when a stimulus tone pip lasted beyond the time of occurrence of the response. On the other hand, in many cases the response was larger or had a lower threshold for some durations than others. Figure 3 shows an example in which pulses of 2 to 3 msec were strongly preferred over shorter or longer ones (solid curve); in other cases, the threshold fell monotonically up to a duration of 3 to 5 msec (dashed curve).

Unlike many of the early single-unit responses or the positive evoked potentials representing summed activity of the first few auditory neural levels, the late single unit and slow negative evoked potential responses showed poor recovery. Often an interval between stimuli as long as 60 to 100 msec was required before a second late response could even be detected, and as much as 0.2 to 0.5 second was sometimes necessary for full recovery. On the other hand, inhibition of the late response by an earlier louder sound, which elicited only an early response, lasted only 10 to 15 msec.

The late response involves circuitry different from or additional to that of the early response, as demonstrated by moving the signal around the bat's head in the horizontal plane; the late response often showed changes in sensitivity with direction different from those of the early response. Characteristically, but not invariably, the late response was more sharply directional with a sharper drop-off of sensitivity at ipsilateral angles.

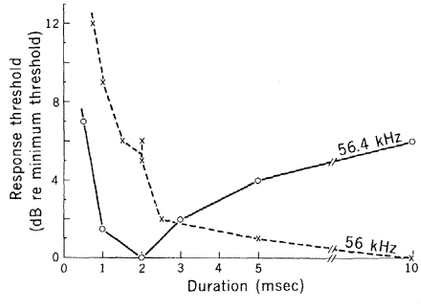

Fig. 3. Threshold for the "late" response of two collicular single units as a function of the duration of the stimulating tone pip.

Whereas many single units showing only an early response were selective for FM sounds (that is, responded only to an FM sound or had a threshold 10 to 30 dB lower for FM than for CF sounds), the late responses showed no preference for FM. A few late-responding units were unresponsive to any FM signal; others had FM thresholds the same as those to a tone pip of the most effective frequency in that sweep. In a few cases, narrow inhibitory fields could be demonstrated to either side of the effective stimulating frequencies, but in other cases such inhibition of the late response was not apparent. In all cases there was inhibition, or absence of the late excitation, at higher intensities near the best frequency of the late response.

The functional significance of these late responses and the neural circuitry responsible for them are not clear. The restriction of response to approximately the frequency of the CF component of the pulse (or, more exactly, to a slightly higher frequency, such as that of an upward Doppler-shifted echo) and the preference for a signal duration of 2 to 3 msec imply that this response behavior is important somehow to the use of the CF component. At the simplest level of interpretation, it appears possible that the late-responding units constitute a population that responds in a certain way (the late response) selectively to a very faint CF echo heard after recovery from inhibition due to the loud outgoing pulse—that is, at a pulse-echo interval of more than 10 to 15 msec or a target distance of about 2 m. This population might serve an alerting function during low-repetition-rate searching flight.

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8. We thank the staff of the Smithsonian Tropical Research Institute, Panama Canal Zone, for their valuable assistance. Supported by NSF grant BNS 76-03068.

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Conformational Changes in 16*S* Ribosomal RNA Induced by 30*S* Ribosomal Subunit Proteins from *Escherichia coli*

Abstract. *Laser light scattering has been used to evaluate conformational differences between free 16*S *RNA and several specific protein-16*S *RNA complexes. Proteins that interact strongly with the 16*S *RNA early in subunit assembly stabilize the RNA chain against unfolding in 1 m*M Mg^{2+} *and actually promote the formation of a more compact tertiary structure in 20 m*M Mg^{2+}. *A vital function of these proteins may therefore consist in altering the configuration of the RNA so that further assembly reactions can take place.*

Assembly of the 30*S* ribosomal subunit of *Escherichia coli* entails the cooperative association of 21 different proteins with a single molecule of 16*S* RNA (*1*). During this process, the ribosomal RNA attains a configuration that is much more compact than in the free state (*2–4*). Although there is little known about the mechanism of folding, sedimentation analysis of assembly intermediates suggested that major changes in RNA conformation occurred only after the association of 10 to 15 proteins with the nucleic acid chain (*2*). Our present results, however, show that folding of the 16*S* RNA begins upon the binding of proteins S4, S7, S8, and S15, either singly or in combination, in the very first stages of subunit assembly (*5*). Changes in RNA structure were followed by the technique of laser light scattering (*6*), which yields precise values of the translational diffusion constant, *D*, a sensitive indicator of variation in macromolecular size and shape.

Diffusion constants for 16*S* RNA and native 30*S* particles were determined in LM buffer (1 m*M* $MgCl_2$; see Table 1 legend) and in TMK buffer (20 m*M* $MgCl_2$; see Table 1 legend), a solvent that was originally developed to optimize subunit assembly in vitro (*1*). It is apparent from Table 1 that the 30*S* subunit exhibits a larger $D^{o}_{20,w}$ than free 16*S* RNA in both ionic environments. A similar relation exists between $D^{o}_{20,w}$ values of the 50*S* subunit and the 23*S* RNA (data not shown). Our findings provide direct evidence that ribosomal subunits are more compact than their constituent RNA's even though their mass is 50 to 60 percent greater (*7*). Indeed, the $D^{o}_{20,w}$ of a particle with the same shape and density as the 16*S* RNA, but with the molecular weight of the 30*S* subunit (*8*), would be 15 percent lower than that of the RNA alone, since D^{o} is inversely proportional to $(M)^{1/3}$ in such cases. The values obtained for the 30*S* subunit, however, are from 3 to 11 percent higher than for the 16*S* RNA. Diffusion constant measurements can thus be used to discriminate between increases in the folding of a molecule and increases in its mass.

The pronounced difference in the $D^{o}_{20,w}$ of 16*S* RNA in the two buffers can be ascribed primarily to unfolding of the nucleic acid chain at low Mg^{2+} concentrations. This process is also reflected by a decrease in the sedimentation coefficient of 16*S* RNA between 20 and 1 m*M* Mg^{2+} (*4, 9*). The conformation of the 30*S* subunit is comparatively insensitive to changes in Mg^{2+} concentration, however, supporting the general view that ribosomal proteins are essential in maintaining the compact structure of the particle (*3, 4*).

We next investigated the interaction of 16*S* RNA with 30*S* subunit proteins S4, S7, S8, and S15, all of which bind to specific and independent sites in the nucleic acid molecule (*10*). Since one or a small number of ribosomal proteins contribute little to the mass of the complexes, variations in D^{o} are dominated by changes in RNA conformation. In LM buffer, $D^{o}_{20,w}$ values of the individual ribonucleoproteins were significantly higher than that of free 16*S* RNA (Table 1). By contrast, the $D^{o}_{20,w}$ of a mixture containing S5, a protein that does not associate independently with the RNA, was identical to that of 16*S* RNA alone.

Table 1. Diffusion constants of the 16*S* RNA, protein-16*S* RNA complexes, and the 30*S* subunit. Proteins S4, S7, S8 and S15, 16*S* RNA, and 30*S* ribosomal subunits were prepared from *E. coli* MRE600 (*18*). The 16*S* RNA and 30*S* subunits were suspended in TMK buffer (50 m*M* tris-HCl, *p*H 7.6, 20 m*M* $MgCl_2$, 350 m*M* KCl, 1 m*M* dithiothreitol) and dialyzed against either TMK or LM buffer (10 m*M* tris-HCl, *p*H 7.6, 1 m*M* $MgCl_2$, 100 m*M* KCl, 1 m*M* dithiothreitol). Reconstituted complexes were formed by incubating an excess of protein with 16*S* RNA at a concentration of 500 μg/ml in TMK for 30 minutes at 40°C (*18*) and then dialyzed against the appropriate measuring buffer. Control experiments confirmed that protein bound in 20 m*M* Mg^{2+} remained associated with the RNA in 1 m*M* Mg^{2+}. Dialyzed mixtures were diluted and filtered through Millipore GS membranes to remove free protein (*19*) and particulate matter. After a brief incubation at 40°C, the samples were cooled to 20°C, and values of D_{20} were determined by laser light scattering (*6*). Results from several runs on different preparations were corrected for solvent viscosity and averaged to give $D_{20,w}$. Since $D_{20,w}$ was generally independent of sample concentration from 50 to 500 μg/ml, the averaged value was taken as $D^{o}_{20,w}$. Data for complexes that contained less than 0.75 mole of each protein per mole of RNA, or that contained degraded RNA following light scattering, were discarded. Standard deviations include errors within individual runs as well as variations from one preparation to another. The number of samples analyzed for each value is indicated in parentheses.

Sample	$10^{-7} \times D^{o}_{20,w}$ (cm²/sec)	
	LM buffer	TMK buffer
16*S* RNA	1.77 ± .01 (4)	1.96 ± .01 (3)
30*S* subunit	1.97 ± .01 (4)	2.02 ± .02 (4)
S5 plus 16*S* RNA	1.77 ± .03 (2)	
S4–16*S* RNA	1.88 ± .01 (8)	1.96 ± .01 (5)
S7–16*S* RNA	1.83 ± .01 (7)	2.02 ± .03 (2)
S8–16*S* RNA	1.95 ± .01 (5)	1.96 ± .01 (2)
S15–16*S* RNA	1.83 ± .01 (6)	2.04 ± .02 (3)
S4, S7–16*S* RNA	1.94 ± .01 (8)	2.09 ± .03 (1)
S4, S8–16*S* RNA	1.84 ± .01 (4)	2.07 ± .03 (2)
S4, S15–16*S* RNA	1.92 ± .01 (6)	2.16 ± .01 (2)
S8, S15–16*S* RNA	1.90 ± .01 (6)	2.10 ± .02 (2)
S4, S7, S15–16*S* RNA	1.89 ± .01 (7)	2.04 ± .03 (4)
S4, S7, S8, S15–16*S* RNA	2.01 ± .01 (3)	2.15 ± .03 (1)

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