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Scalar Timing Varies With Response Magnitude in Classical Conditioning of the Nictitating Membrane Response of the Rabbit (*Oryctolagus cuniculus*)

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The present experiment was aimed at characterizing the timing of conditioned nictitating membrane (NM) movements as function of the interstimulus interval (ISI) in delay conditioning for rabbits (*Oryctolagus cuniculus*). Onset latency and peak latency were approximately, but not strictly, scalar for all but the smallest movements (<.10 mm). That is, both the mean and standard deviation of the timing measures increased in proportion to the ISI, but their coefficients of variation (standard deviation/mean) tended to be larger for shorter ISIs. For all ISIs, the absolute timing of the NM movements covaried with magnitude. The smaller movements (approximately, .11-.50 mm) were highly variable, and their peaks tended to occur well after the time of US delivery. The larger movements (>.50 mm) were less variable, and their peaks were better aligned with the time of US delivery. These results are discussed with respect to their implications for current models of timing in eyeblink conditioning.

Keywords: conditioning, timing, rabbit, interstimulus interval

The present experiment was conducted to determine whether conditioned responses (CRs) in the rabbit nictitating membrane (NM) preparation show scalar timing. Scalar timing is a proportional increase in the mean and variance in the time course of CRs as the interstimulus interval (ISI) between the onset of the conditioned stimulus (CS) and onset of the unconditioned stimulus (US) increases (Gallistel & Gibbon, 2000; Gibbon, 1977; Lejeune & Wearden, 2006). In previous NM studies, evidence of scalar timing has been seen in the location of the maximal closure of the NM. When measured on CS-alone test trials to avoid intrusion by the unconditioned response (UR), the maximum closure of the NM measured relative to CS onset—denoted as the "peak latency" —appears around the time that the US occurred on CS-US trials (Smith, 1968). Moreover, the variance of peak latency tends to increase in proportion to the ISI (White, Kehoe, Choi, & Moore, 2000).

Although scalar timing of the NM response might appear to be a settled matter, previous studies were restricted to NM movements that exceeded a minimum criterion, often .50 mm. More recent findings have suggested that NM movements well below the .50-mm criterion also show timing characteristics similar to their larger counterparts (Kehoe, Ludvig, Dudeney, Neufeld, & Sutton, 2008). This study, however, only used a single ISI (500 ms), and, hence, could not reveal whether the timing of subcriterial movements was scalar.

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For purposes of neural recording and quantitative modeling, a characterization of the temporal characteristics of small movements and their relationship to the timing of larger movements is significant in two respects. First, early in training, the appearance of the small movements may provide the earliest behavioral indication of changes in conditioning pathways. Second, while the scalar nature of peak latencies has been evident in larger movements throughout training (Millenson, Kehoe, & Gormezano, 1977; Smith, 1968), it is unknown whether scalar timing is an invariant feature of conditioned movements or itself is shaped during training. An examination of the timing of movements in relationship to their size over training would help resolve these two questions.

To characterize the timing of NM movements across all sizes, the present experiment was conducted using ISIs of 250 ms, 500 ms, and 1000 ms, which respectively produce rapid, moderate, and slow rates of CR acquisition in delay conditioning (Kehoe & Macrae, 2002). So that timing of the NM movements uninterrupted by either CS offset, the US, or the UR could be revealed, the experimental add two additional features:

First, the CS duration was equated across groups at 1500 ms, which unconfounded CS duration and the time of its offset from ISI. This duration allowed the bulk of each CR, especially its peak, to occur before the CS terminated. Although the extension of the CS past the US was inversely related to the ISI, post-US extensions of the CS have had only modest effects on CR acquisition in rabbits, sometimes positive (Kehoe, 2000; McNish, Betts, Brandon, & Wagner, 1997) and sometimes negative (McNish et al., 1997; Schneiderman, 1966). In rat fear conditioning, negative effects of post-US extensions have been far smaller than corresponding pre-US extensions (Albert, Ricker, Bevins, & Ayres, 1993; Ayres & Albert, 1990).

Second, each training session contained a mixture of 70% CS-US pairings and 30% CS-alone trials, allowing for more fre-

quent sampling of the full CR time course. This schedule only slightly reduces the rate of CR acquisition relative to a schedule containing 90% CS-US pairings and 10% CS-alone trials (Kehoe et al., 2008).

Method

Subjects and Apparatus

The subjects were 24 female, albino rabbits (*Oryctolagus cuniculus*), 70–80 days old, weighing around 1.5 kg on arrival. The apparatus was based on that of Gormezano (1966, cf. Kehoe & Joscelyne, 2005). The CS was a 1500-ms, 1000-Hz, 83-dB (SPL, C scale) tone. Background noise (76 dB, SPL, C scale) was provided by white noise and a ventilating fan. The US was a 50-ms, 3-mA, 50-Hz AC current delivered via wound clips positioned 10 mm behind the dorsal canthus of the right eye and 15 mm below the eye. To minimize distortion and slippage in transduction of the NM movement, no eye straps were used, and the transducer was hard coupled to a small loop of surgical suture in the membrane via a stainless steel, ball-and-socket armature (Gormezano & Gibbs, 1988). The ISI was either 250, 500, or 1000 ms, and the mean intertrial interval was 60 s (range 50–70 s).

Procedure

Each rabbit was prepared by suturing a silk loop (000) into the NM of the right eye under local anesthetic (proxymetacaine hydrochloride). The next day, the rabbits were adapted to the conditioning apparatus for 60 min. They were then assigned randomly to three groups ($n = 8$) designated as Groups 250, 500, and 1000 in accordance with their ISIs. (For Group 250, one rabbit was removed as a result of an eye infection.) All groups received 16 sessions of training, each divided into 6 blocks of 10 trials. Each block contained a mixture of seven CS-US trials and three CS-alone trials, in which no more than two CS-alone trials occurred consecutively.

Statistical Tests

Planned statistical contrasts used a Type I error of .05 (O'Brien & Kaiser, 1985), and partial eta squared (η_p^2) measured effect size (Cohen, 1973). This measure equals the proportion of explained variance: $SS_{effect}/(SS_{effect} + SS_{error})$. According to Cohen (1988), $\eta_p^2 = .010$, .059, and .138 imply small, medium, and large effects, respectively.

Results

The top and middle rows of Figure 1 depict the relationship between the timing and size of NM movements on a logarithmic scale. The top row plots the onset latency for each NM movement that was detected within 2000 ms following CS onset on CS-alone trials. Onset latency was defined as the time between CS onset and the initiation of NM closure (Marshall-Goodell, Schreurs, & Gormezano, 1982). The middle row shows the corresponding plots for peak latency, which was defined as the time from CS onset to the point of maximum closure. Movements as small as .06 mm were included in both sets of plots. Each panel shows all the latencies for all these movements across all days for all the subjects in a group.

Inspection of these plots reveals that, as the magnitude of the movements increased, their timing changed. In Groups 250 and 500, both the onset latencies and peak latencies became more tightly clustered as the magnitude increased. Group 1000's timing remained variable throughout training, although the onset latencies appeared to decline.

Magnitudes of NM movements tend to increase across CS-US pairings (Garcia, Mauk, Weidemann, & Kehoe, 2003; Kehoe et al., 2008). Thus, changes in timing across acquisition may reflect changes in the mixture of different-sized movements. To show these changes in the present experiment, the bottom row of panels in Figure 1 plots the magnitude of movements on successive CS-alone trials across all days for each group. These plots confirm recent findings, even while larger responses appear as training progresses, there remain many smaller responses in the mix (Gallistel, Fairhurst, & Balsam, 2004; Kehoe et al., 2008).

To reveal any changes in timing of movements of different sizes, each rabbit's movements were partitioned into the seven ranges of magnitude: .06 –10, .11-.25, .26-.50, .51–1.00, 1.01–2.00, 2.01–4.00, and 4.01–8.00 mm (Garcia et al., 2003). For successive movements within each range, straight lines were fitted to each rabbit's onset latencies and peak latencies. Onset latencies showed slight negative slopes (−16 ms between successive movements), as did the peak latencies (−7 ms). However, statistical tests failed to confirm that the slopes differed from zero, all $ps > .40$, nor were there any differences in the slopes as a function of ISI. Thus, to a first approximation, the timing of movements within each size range appeared to be stable.

As the basis for statistical testing of the relationship between the magnitude of NM movements and their timing characteristics, the mean and standard deviation of the onset latency and peak latency for each rabbit's movements within each size range were computed. The top row of panels in Figure 2 shows, respectively, the average onset latency (M), the average standard deviation (*SD*), and the average coefficient of variation (CV), which is the ratio of the *SD*/M. A CV that is constant across ISIs is usually construed as evidence of scalar timing (White et al., 2000). In each panel, a separate set of points is shown for each group. For all but the smallest movements, the best-fitting logarithmic line is superimposed to help see trends across magnitudes. The second row of panels shows the corresponding results for peak latency.

The smallest movements (.06 mm –.10 mm) were excluded from the fits, because their means and standard deviations appeared to have been strongly biased by spontaneous flutters unrelated to CS-US pairings and unrelated to the ISI. The likelihood of these spontaneous movements was estimated by examining the first five CS-alone trials in which few, if any, movements would have resulted from CS-US pairings. The percentage of these trials that contained a movement of .06-.10 mm was 11%. Across groups, the peak latencies of these movements appeared uniformly distributed between 165 ms (minimum) to 1925 ms (maximum) with a mean near the middle of the 2000-ms observation interval (M = 1101 ms). Any apparent differences in either the onset latencies or peak latencies across groups were unsystematic and failed to attain statistical significance ($ps > .05$).

For the next largest range of movements (.11 mm-.25 mm), some temporal differentiation across ISIs was apparent, although there was probably a contribution from spontaneous flutters. Examination of the first five CS-alone trials revealed that 9% of them

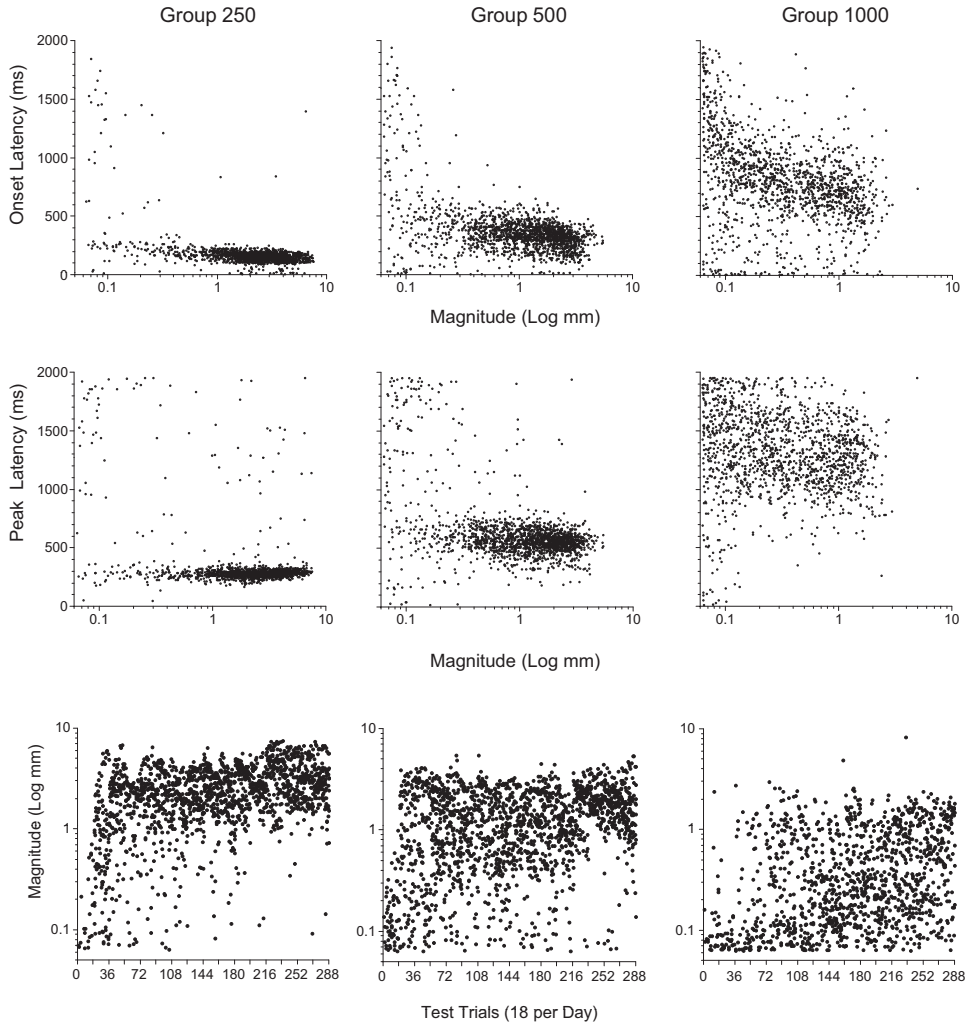


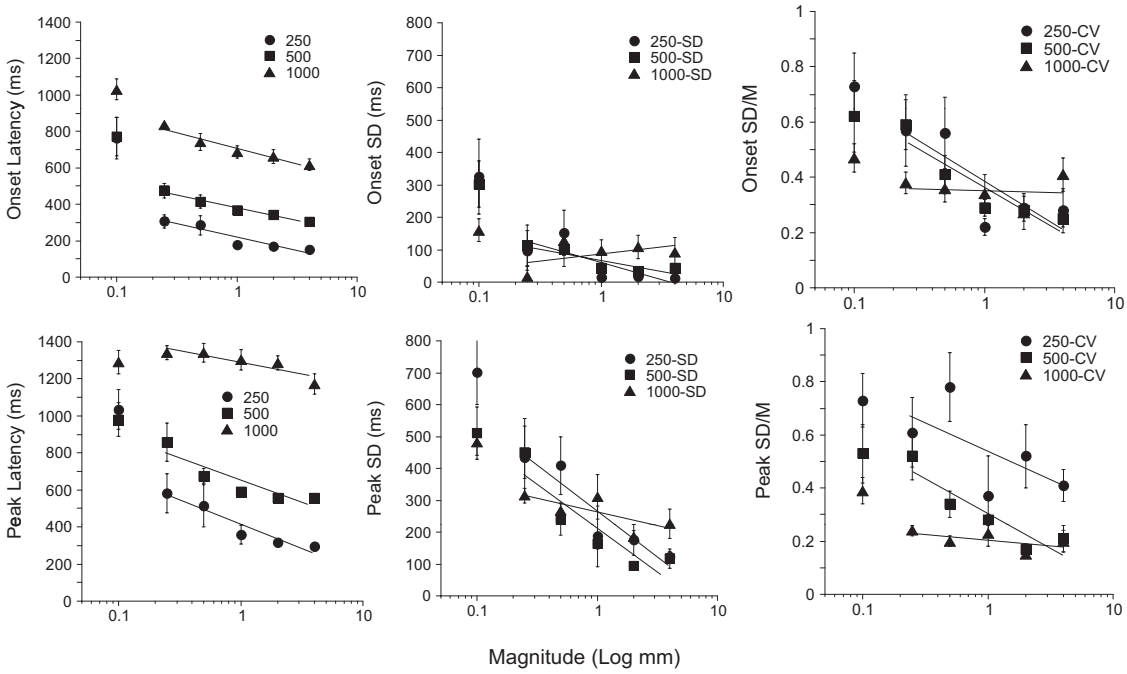
Figure 1. Onset latencies (top row) and peak latencies (middle row) plotted as a function of their $\log_{10}$ magnitude for all subjects that received the 250-ms, 500-ms, and 1000-ms ISIs, respectively. The lower panels plot the magnitude of all detectable NM movements (>.06 mm) as function of successive CS-alone test trials for each group.

contained movements in that size range, again with a fairly even distribution (minimum = 155 ms, maximum = 1905 ms, M = 821 ms). For larger movements, the timing of the movements became even more differentiated, and the contribution of spontaneous movements appeared to be negligible. In the range .26 mm-.50 mm, only 1% of the first five CS-alone trials contained spontaneous movements. For movements > .50 mm, virtually none of them appeared to have been spontaneous flutters.

Inspection of the left-hand panels in Figure 2 reveals that, with the exception of the smallest movements, the mean onset latencies and peak latencies increased significantly as function of ISI, $F(1, 20) = 118.45, 132.89$, $ps < .01$, $\eta_p^2 = .86, .87$. Furthermore, both onset latencies and peak latencies decreased significantly as the magnitudes rose, $F(1, 20) = 61.33, 22.73$, $ps < .01$, $\eta_p^2 = .75, .53$. Averaging across groups, the onset latencies decreased from 100% of the ISI for movements in the .11 mm-.25 mm range down to 61% of the ISI for movements in the largest range (>4.01 mm). The peak latencies declined from 179% to 116% of the ISI.

Inspection of the center panels in each row suggests that, with the exception of the smallest movements, variability (*SD*) in onset latency was relatively constant across both ISIs and magnitudes. Despite this appearance, there was a main effect of magnitude; the variability in onset latency decreased as magnitudes rose, $F(1, 20) = 30.90$, $p < .01$, $\eta_p^2 = .61$. In the case of peak latency, there was a more obvious decline in their variability across magnitudes, $F(1, 20) = 44.36$, $p < .01$, $\eta_p^2 = .69$. Any apparent differences between ISIs in the variability of either onset latencies or peak latencies were not significant. $ps > .05$.

The CVs, which are shown in the right-hand panels, showed a complex pattern. On the one hand, the CVs for the onset latencies significantly declined across magnitudes, $F(1, 20) = 27.45$, $p < .01$, $\eta_p^2 = .58$. Any apparent differences related to the ISI failed to reach statistical significance, $F(1, 20) = 4.05$, $p > .05$, $\eta_p^2 = .17$. In contrast, the CVs for peak latencies showed a downward linear trend across ISI, $F(1, 20) = 32.40$, $p < .01$, $\eta_p^2 = .62$. Group 250 showed a larger CV than Group 500, which generally showed a



	Group 250		Group 500		Group 1000	
	First 25	Last 25	First 25	Last 25	First 25	Last 25
			Magnitude			
Mean (mm)	1.24	3.20	0.93	1.71	0.33	0.66
SD (mm)	0.82	1.24	0.57	0.86	0.34	0.43
			Onset Latency			
Mean (ms)	290	159	446	408	864	781
SD (ms)	342	33	276	139	479	309
CV: SD/M	1.19	0.21	0.61	0.30	0.58	0.40
			Peak Latency			
Mean (ms)	492	319	741	614	1310	1304
SD (ms)	479	130	332	141	446	273
CV: SD/M	0.98	0.35	0.46	0.20	0.35	0.21

Figure 2. The top row of panels plots measures of onset latency for each of seven magnitude ranges (0–.10, .11–.25, .26–.50, .51–1.00, 1.01–2.00, 2.01–4.00, and 4.01–8.00 mm, respectively). In each panel, there is a separate line fitted to each group's data. Reading left to right, the panels show, respectively, the mean (M), the average standard deviation (*SD*), and average coefficient of variation (CV = *SD*/M). The error bars represent the standard error of the mean. The second row of panels shows the corresponding plots for peak latency. The bottom panel lists the mean and standard deviation of the magnitude, onset latency, and peak latency for the first 25 and last 25 NM movements for each group. For onset latency and peak latency, the average coefficient of variation (CV = *SD*/M) is also listed.

larger CV than Group 1000. In addition to the ISI effect, the CVs for peak latency declined across magnitudes, $F(1, 20) = 16.10$, $p < .01$, $\eta_p^2 = .45$. Any apparent interaction of ISI with magnitude for peak latencies was not statistically significant, $F(1, 20) = 3.39$, $p > .05$, $\eta_p^2 = .14$.

To examine timing as the mix of magnitudes changed across training, the magnitudes, onset latencies, and peak latencies for each rabbit's first 25 movements and last 25 movements were compared. The averages of the computations for each group are listed at the bottom of Figure 2. As previously seen in Figure 1, the mean mag-

nitudes increased from the start to end of acquisition, $F(1, 20) = 25.61$, $p < .01$, $\eta_p^2 = .56$, and decreased across ISIs, $F(1, 20) = 33.36$, $p < .01$, $\eta_p^2 = .63$. With respect to onset latency, there was both a decrease in the mean across acquisition, Fs $(1, 20) = 4.77$, $p < .05$, $\eta_p^2 = .19$, and an increase across ISIs, $F(1, 20) = 166.73$, $p < .01$, $\eta_p^2 = .89$. The *SD* also contracted over training, $F(1, 20) = 37.63$, $p < .01$, $\eta_p^2 = .65$, and increased across ISI, $F(1, 20) = 22.24$, $p < .01$, $\eta_p^2 = .53$. For the first 25 movements, the average CVs for onset latency were relatively large, often exceeding .50, but showed a downward linear trend across ISIs, $F(1, 20) = 46.50$, $p < .01$, $\eta_p^2 = .70$. By the last 25 movements, however, the CVs were smaller and showed a significant upward trend across ISIs, specifically .21, .30, and .40 for Groups 250, 500, and 1000, respectively, $F(1, 20) = 4.80$, $p < .05$, $\eta_p^2 = .19$.

The mean peak latency decreased only slightly across training, $F(1, 20) = 4.14$, $p > .05$, $\eta_p^2 = .17$, while showing an upward trend across ISIs, $F(1, 20) = 183.94$, $p < .01$, $\eta_p^2 = .90$. The *SD* of the peak latencies also contracted over training, $F(1, 20) = 35.65$, $p < .01$, $\eta_p^2 = .64$, but the *SD* was showed no significant effect of ISI at either point in training. Over the last 25 movements, for example, the SDs for Groups 250, 500, and 1000 ms were, respectively, 130, 141, and 273 ms, but the upward trend was not significant, $F(1, 20) = 3.60$, $p > .05$, $\eta_p^2 = .15$. As was the case for CVs for onset latency, the CVs for peak latency during the first 25 movements showed a downward linear trend, $F(1, 20) = 40.96$, $p < .01$, $\eta_p^2 = .67$. By the last 25 movements, the downward trend in CVs had largely disappeared, $F(1, 20) = 1.27$, $p > .05$, $\eta_p^2 = .06$.

Discussion

The present experiment was aimed at characterizing the timing of NM movements across their full range of magnitudes, including movements well below the conventional criterion of .50 mm. More specifically, the experiment was aimed at determining whether timing is scalar for all sizes and whether timing for each size is shaped during training. The present experiment revealed the following major findings:

(1) Timing of NM movements as measured by onset latency and peak latency was approximately scalar for all but the smallest movements (<.10 mm). That is, both the mean and standard deviation of the timing measures showed increases proportional to the ISI.

(2) The absolute timing of the NM movements differed across magnitudes. The smaller movements were highly variable. Their peaks, on average, tended to occur well after the time of US delivery. The larger movements, particularly for the 250-ms and 500-ms ISIs, were less variable in their timing, and their peaks were better aligned with the time of US delivery.

(3) These size-related features of timing, within each size range, were approximately constant over training.

(4) Over training, the distribution of magnitudes trended upward but nevertheless remained highly variable. Hence, changes in averages of onset latency and peak latency over training appeared to reflect changes in the mix of sizes.

(5) The coefficients of variation (CV = *SD*/M) showed a complex pattern. For early movements early in training, the CVs for onset latency and peak latency showed downward trends across ISIs, However, for movements later in training, the CVs for onset latency showed an upward trend, while the CVs for peak latencies had largely converged on smaller values. Thus, timing was not strictly scalar across ISIs.

Whether the timing of NM movements is approximately or strictly scalar, the pattern of onset latencies, peak latencies, and magnitudes suggests that there is a delicate interplay within the neural mechanisms that govern the adaptive function of NM timing. This adaptive function requires a balance between maintaining current vision (eyelid open) and protecting the eye (eyelid closed). In the present results, larger movements, which would provide greater protection, were better aligned with the time of the anticipated threat, that is, US delivery. Conversely, smaller movements, which provide little protection to the eye, tended to start later and peak after the time of US delivery. To the extent that the magnitude of the movement is a product of the strength of the underlying association and its current activation, the system appears tuned to protect the eye when the anticipation of threat is strong but to maintain vision when there is little anticipation of injury. Along this same line of argument, the variability in the magnitudes even late in training also suggests the system is tuned to maintain current vision even when the threat could be well anticipated.

The effect of the ISI on the timing of NM movements, even very tiny ones, is consistent with spectral timing models in which the acquisition and timing of conditioned NM movements are mediated by the progressive activation of elements initiated by the CS (Desmond & Moore, 1988; Grossberg & Schmajuk, 1989; Kehoe, Horne, & Macrae, 1995; Sutton & Barto, 1990). In these models, each element is assumed to develop associative strength in proportion to its level of activation at the time of the US. Therefore, the elements that occur around the time of US delivery gain the greatest associative strength. During subsequent presentations of the CS, the magnitude of the NM movement at any point in time reflects the summation of the associative strengths of the elements in that time zone, and the movement's peak tends to occur near the time of US delivery, where there had been the greatest overlap of elements with the US. The roughly scalar properties of conditioned movements can be explained by assuming that the elements overlap and form an array of increasingly broader and more variable periods of activation. Thus, the earliest elements rise and fall rapidly, which yield the tightly timed movements produced by shorter ISIs. Later elements rise and fall more slowly, which yield the broader, more variable movements produced by longer ISIs. For these models, the size-related differences in timing of movements at all ISIs seen here could be addressed in the variability in their stimulus activation or response generation mechanisms.

At a neural level, such a spectrum may arise from the progressive time delays introduced as CS input is spread through the cerebellar cortex via the synapses among mossy fibers, granule cells, parallel fibers, and Purkinje cells (Buonomano & Mauk, 1991; Mauk, Medina, Nores, & Ohyama, 2000; Moore & Choi, 1997). In particular, the scalar timing of conditioned NM movements may be explained by the planar nature of Purkinje cells coupled with their dendritic morphology (Ito, 1984; Steuber &

Willshaw, 2004). The first inputs from the parallel fibers activated by a CS would converge near the base of Purkinje cells. Succeeding inputs would then ascend the dendritic tree as time elapses. Recently, in fact, ISI-dependent activity has been observed in individual Purkinje cells (Jirenhed, Bengtsson, & Hesslow, 2007).

The detection of ISI effects on the timing of even tiny movements suggests that descending portions of the cerebellar paths that ultimately generate the NM movement may be best modeled as a continuous process—for example, a leaky integrator—rather than an all-or-none process in which a discrete conditioned movement occurs when the level of underlying activation rises above a threshold value.

For methodological purposes, the effects of ISI on even tiny NM movements can guide which movements can be safely counted as CRs. The definition of a CR is limited by the same basic constraint as in all signal detection tasks. Any particular criterion is a compromise between maximizing the count of CRs (true positives) versus minimizing the inclusion of spontaneous movements (false positives). A relatively conservative criterion (.50 mm) has been used historically (Gormezano, 1966), but the present results suggest that a more liberal criterion (.25 mm) can be used with only a tiny rise in false positives. In fact, for the external eyelid of the rabbit, a criterion of .30 mm has been already been used (e.g., Garcia et al., 2003).

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