Behavioral Neuroscience
2007, Vol. 121, No. 4, 808–813

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0735-7044/07/$12.00 DOI: 10.1037/0735-7044.121.4.808

BRIEF COMMUNICATION

# Time-Specific Extinction and Recovery of the Rabbit's (*Oryctolagus cuniculus*) Conditioned Nictitating Membrane Response Using Mixed Interstimulus Intervals

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Extinguishing a conditioned response (CR) has entailed separating the conditioned stimulus (CS) from the unconditioned stimulus (US). This research reveals that elimination of the rabbit nictitating membrane response occurred during continuous CS–US pairings. Initial training contained a mixture of 2 CS–US interstimulus intervals (ISIs), 150 ms and 500 ms. The CRs showed double peaks, one for each ISI. When the 150-ms ISI was removed, its CR peak showed 2 hallmarks of extinction: a decline across sessions and spontaneous recovery between sessions. When a further stage of training was introduced with a distinctive CS using the 150-ms ISI, occasional tests of the original, extinguished CS revealed another hallmark of extinction, specifically, strong recovery of the 150-ms peak. These results support both abstract and cerebellar models of conditioning that encode the CS into a cascade of microstimuli, while challenging theories of extinction that rely on changes in CS processing, US representations, and contextual control.

*Keywords:* conditioning, rabbit, extinction, recovery, interstimulus interval

The present study combined two effects seen in classical conditioning of the rabbit's nictitating membrane (NM) response. They are *time-specific extinction* (Joscelyne & Kehoe, 2007; Kehoe & Joscelyne, 2005) and *concurrent recovery* (Macrae & Kehoe, 1999; Weidemann & Kehoe, 2003, 2004, 2005).

Time-specific extinction entails the elimination of a conditioned response (CR) in one portion of a conditioned stimulus (CS) while the CS as a whole is still paired with the unconditioned stimulus (US; Boneau, 1958; Coleman & Gormezano, 1971; Yeo, Lobo, & Baum, 1997). For example, Kehoe and Joscelyne (2005) conducted initial conditioning in which a single, 1,400-ms tone CS was paired with a 50-ms electrodermal US. Instead of using a constant interstimulus interval (ISI) between CS onset and US onset, they randomly mixed two ISIs, specifically, 200 ms and 1,200 ms. When tested with the CS alone, the CRs showed two peaks, one timed to each point of US delivery on paired trials. In a second stage, CS–US pairings were continued, but with only the 1,200-ms ISI. Consequently, the CR peak near the 200-ms point displayed three hallmarks of conventional extinction in NM conditioning: (a) progressive disappearance over sessions; (b) spontaneous, overnight recovery; and (c) rapid reacquisition when the 200-ms ISI was reintroduced in a third stage of training. At the same time, the CR peak based on the 1,200-ms ISI grew throughout the experiment. In a complementary experiment, the 1,200-ms peak, but not the 200-ms peak, was eliminated when second-stage training was conducted with only the 200-ms ISI.

Time-specific extinction is consistent with models in which the CS is encoded as a series of microstimuli, each capable of acquiring associative strength according to its temporal distance from the US (e.g., Grossberg & Schmajuk, 1989; Kehoe & Napier, 1991a; Pavlov, 1927, pp. 103-104; Sutton & Barto, 1990; Vogel, Brandon, & Wagner, 2003). As one possible neural basis for microstimuli in NM conditioning, different populations of granule cells in the cerebellar cortex may become active at different times during mossy fiber activity initiated by a CS (Mauk & Buonomano, 2004; Medina, Nores, Ohyama, & Mauk, 2000). During CS–US pairings, the synapses of these granule cells on Purkinje cells undergo a change that is expressed in CR timing.

At a minimum, time-specific extinction suggests that the theoretical and neural mechanisms for CR timing and extinction are intimately linked. If extinction entailed a generalized downregulation of either CS processing or CR generation, then time-specific extinction could not occur because the CS is still paired with the US and CRs are still being generated. Time-specific extinction also challenges context-based theories of extinction. In conventional extinction, the removal of the US could produce a large change in the animal's internal context. This change in context could yield an immediate generalization decrement in responding (Capaldi, 1994), and with further extinction training, the US-absent context could become a conditional cue for expressing an inhibitory association acquired by the CS (Bouton, 2004).

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Preparation of this article was supported by Australian Research Council Grant DP0344082.

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In the previous demonstrations of time-specific extinction, the US was present throughout all stages of training. In fact, the number and spacing of CS and US presentations were fixed throughout each experiment. Moreover, there were no alterations to the global context (e.g., ambient noise, ambient light). Thus, the conventional sources of contextual change between acquisition and extinction were not available.

In defense of context-based theories, a change in the pattern of ISIs might progressively alter the internal context. Although it is perhaps impossible to eliminate all changes in the ISI pattern, reductions in the magnitude of these changes should at least slow down extinction. The recent demonstrations of time-specific extinction used a mixture of two ISIs (Joscelyne & Kehoe, 2007; Kehoe & Joscelyne, 2005) so that the elimination of one ISI was not confounded with the introduction of a new, unfamiliar ISI. Similarly, the CS duration was fixed throughout the experiment so that it could not provide a possible source of contextual change. Contrary to a context-based theory, the rates of extinction, spontaneous recovery, and reacquisition overlapped those of conventional extinction (cf. Napier, Macrae, & Kehoe, 1992).

The present experiment was aimed at further reducing the possible contextual change arising from change in the ISI pattern. Two refinements were introduced: First, the difference between ISIs was reduced. Previously, Kehoe and Joscelyne (2005) had used a mixture of 200-ms and 1,200-ms ISIs, the former being a nearly optimal ISI for the NM preparation and the latter being well outside the optimal range. In the present experiment, the ISIs were 150 ms and 500 ms, which bracket the optimal range and yield similar rates of CR acquisition (Kehoe & Macrae, 2002).

Second, a large number of CS-alone trials were presented in order to further obscure the change in the ISI pattern. In previous mixed-ISI studies, the likelihood of the US occurring at either ISI was 50% on any given trial. However, once one of the ISIs had been removed, the likelihood of the US being delivered at the other ISI rose to 100%. In the present experiment, the initial mixture of trials consisted of one third with a 150-ms ISI, one third with a 500-ms ISI, and one third with the CS alone. Subsequently, to test for time-specific extinction, the 150-ms ISI was replaced by more 500-ms ISI trials. Thus, the likelihood of a 500-ms ISI rose to 67%, but there remained a 33% likelihood that the US would not occur.

Concurrent recovery of an extinguished CR occurs when a new CS from a different sensory modality is paired with the US. For example, Weidemann and Kehoe (2004) conducted an experiment in which stimuli from three different modalities (tone, light, and tactile) were assigned to roles as CSA, CSB, and CSC in a counterbalanced fashion. In Stage 1, CSA–US pairings established a CR. In Stage 2, CSA-alone presentations occurred until the observable CR was entirely extinguished. In Stage 3, CSB–US pairings were presented, along with periodic testing of CSA and CSC. As CRs were acquired to CSB, there was strong recovery of extinguished CRs to CSA ($>$ 45% CRs). However, there were no generalized CRs to CSC, which had never been paired with the US ($<$ 5% CRs).

Controls have confirmed that concurrent recovery is separate from other forms of recovery. More familiar forms of recovery—namely, spontaneous recovery, reinstatement, and renewal—occur without any pairings of the US with either the extinguished CS or a new CS. In contrast, concurrent recovery is learning dependent and only emerges as a CR is acquired during pairings of the new CS with the US (Weidemann & Kehoe, 2003, 2004, 2005).

A defender of a context-based theory could argue that the introduction of a new CS and its pairing with the US might together produce a context change. That is, the new pairings could progressively introduce something like a "context of learning" that would replace the "context of extinction," thus leading to a gradual renewal effect. This hypothesis was tested in the present experiment by determining whether concurrent recovery occurs after time-specific extinction. Specifically, the animals were trained with mixed ISIs (150 ms/500 ms) and then underwent time-specific extinction by removing the 150-ms ISI. Finally, to test for concurrent recovery, a new CS was paired with the US at the 150-ms ISI, and the original CS was tested to determine whether the CR peak for the 150-ms ISI reappeared. In this procedure, a CS was always paired with the US, and CRs occurred throughout all stages of the experiment. Thus, the context of learning was always present. Hence, if concurrent recovery requires a change from the context of extinction to the context of learning, recovery should not appear. As is shown, it did.

## Method

### *Subjects and Apparatus*

The subjects were 16 female, albino rabbits (*Oryctolagus cuniculus*), 70–80 days old, weighing around 1.5 kg, housed with free access to food and water.

The apparatus was based on that of Gormezano (1966) and is described in detail by Kehoe and Joscelyne (2005). During training, each subject was restrained in a chamber containing a speaker that provided CSA, specifically, a 1,000-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. A visual stimulus (CSB) was supplied by a 10-Hz flashing of a bank of 12 white light-emitting diodes mounted in front of the rabbit. The US was a 50-ms, 3-mA, 50-Hz AC current delivered via two 9-mm wound clips positioned 10 mm posterior to the dorsal canthus of the right eye and 15 mm below the center of the eye. To record the NM response, a photoelectric transducer was linked to the NM via a silk loop suture in the NM (Gormezano & Gibbs, 1988). Both stimulus events and digitization of the responses were controlled using LabView (Version 7, National Instruments, Austin, TX).

### *Procedure*

Each rabbit was prepared for the experiment by suturing a loop of surgical silk (000) into the NM of the right eye under local anesthetic (proxymetacaine hydrochloride). The next day, the rabbits were placed in the conditioning apparatus for 60 min, but no stimuli were presented. The rabbits were then assigned randomly to either of two groups ($n = 8$) designated as E-500 and Control. Group E-500 received three stages of training, each lasting 10 days. Group Control received only Stages 1 and 2.

During Stage 1, both groups received mixed-ISI training with CSA. In each session, there were three types of trials presented: (1) 20 CSA–US pairings at a 150-ms ISI (A150+), (2) 20 CSA–US pairings at a 500-ms ISI (A500+), and (3) 20 presentations of CSA alone (A–). The three types of trials were randomized such that no

more than three trials of one type occurred consecutively. In Stage 2's sessions, Group E-500 had the 20 A150+ trials replaced with 20 A500+ trials, and Group Control continued to receive mixed-ISI training. The mean intertrial interval was 60 s (range = 40–80 s).

In Stage 3's sessions, Group E-500 received 20 CSB–US pairings at the 150-ms ISI (B150+) and 3 interspersed A– trials. This schedule was based on previous demonstrations of concurrent recovery (Macrae & Kehoe, 1999). The mean intertrial interval was 156 s (range = 80–240 s).

### *Response Definition and Statistical Tests*

A CR was defined as any NM extension greater than or equal to 0.5 mm within 500 ms following CS onset. The software identified the two largest CR peaks using a peak detector routine in the LabView7 package. The parameters were set to a width of eight samples (40 ms), a detection threshold of 0.241 volts change from baseline (0.5 mm), and a second derivative threshold of −0.005 volts (Joscelyne & Kehoe, 2007). Statistical tests used a Type I error of 0.05 (O'Brien & Kaiser, 1985).

## Results

### *CR Topographies*

Figure 1 shows the aggregate time course of CRs on A– trials in each group on even-numbered days. Each curve was constructed by averaging the momentary NM readings at successive 5-ms time points after CSA onset across subjects and trials. For each stage, the aggregate curves are arranged with the earliest day at the bottom of the figure and the last day at the top of the figure.

At the end of mixed-ISI training in Stage 1, both groups showed CRs with double peaks, one for each point of US delivery on paired trials. Across subjects, 89% of the CRs contained double peaks. During Stage 2 in Group E-500, removal of the 150-ms ISI progressively eliminated the corresponding peak, whereas the peak based on the 500-ms ISI remained intact. In contrast, Group Control, which continued to receive mixed-ISI training, showed growth in both peaks. In Stage 3, in which Group E-500 received CSB–US training, the CR peak at the 150-ms point during CSA showed strong recovery, whereas the peak at the 500-ms point gradually disappeared.

### *CR Percentages*

For purposes of statistical analysis, Figure 2 shows the likelihood of a CR as a function of five-trial blocks in each stage of training. Each panel contains two curves. One curve shows the mean percentage of A– trials that contained a CR regardless of the location of its peaks. The second curve shows the mean percentage of A– trials that contained a CR with a peak during the first 300 ms of the CS onset. This interval was used by Joscelyne and Kehoe (2007) to capture "early peaks" centered on the 150-ms point. For Stage 3, the panel for Group E-500 also contains a third curve showing the mean percentage of B150+ trials containing a CR.

In Stage 1, overall responding to CSA in both groups rose to mean levels exceeding 90% CRs (± 6%). The likelihood of early peaks also reached levels exceeding 90% CRs (± 10%). In Stage

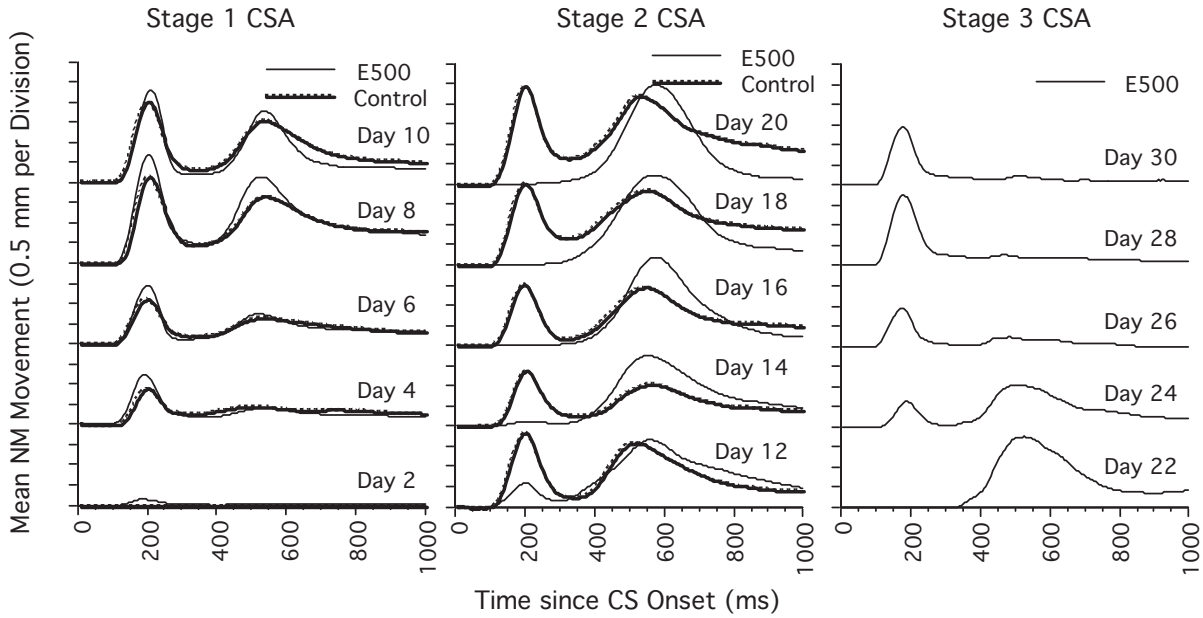


*Figure 1.* Mean momentary magnitudes of the conditioned responses (CRs) at 5-ms intervals on test trials for conditioned stimulus A (CSA) on the even days of Stages 1, 2, and 3, respectively. Days are arranged from earliest at the bottom to latest at the top. NM = nictitating membrane; Group E-500 = trained with both the 150-ms and 500-ms interstimulus intervals (ISIs) and then early CR peaks eliminated by replacing the 150-ms ISI trials with 500-ms ISI trials; Group Control = trained with both the 150-ms and 500-ms ISIs in Stages 1 and 2.

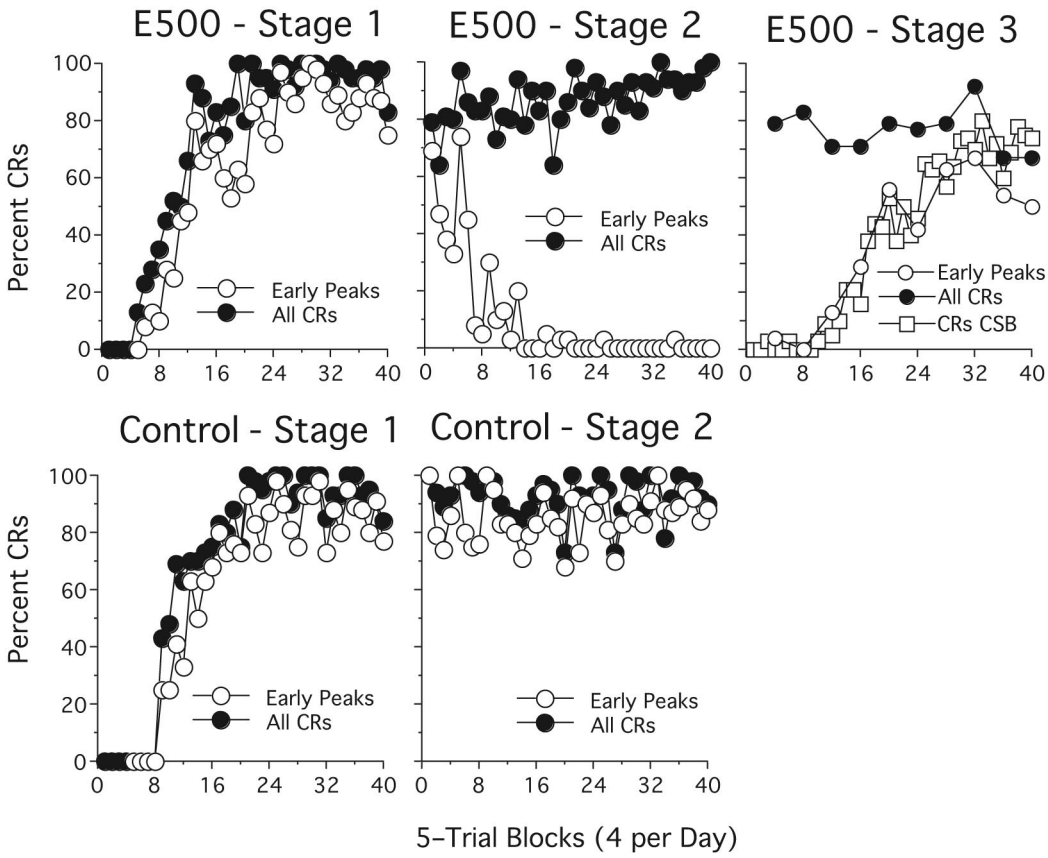


*Figure 2.* Mean percentage of test trials containing (a) a conditioned response (CR) with an early peak during the first 300 ms of conditioned stimulus A (CSA) and (b) a CR during CSA regardless of the location of any peaks. In the panel for Stage 3, there is a curve for the mean percentage of conditioned stimulus B (CSB) trials containing a CR. Group E-500 = trained with both the 150-ms and 500-ms interstimulus intervals (ISI) and then extinguished by replacing the 150-ms ISI trials with 500-ms ISI trials; Group Control = trained with both the 150-ms and 500-ms ISIs in Stages 1 and 2.

2, overall responding to CSA generally remained at high levels in both groups.

Although overall responding to CSA was generally maintained in Stage 2, early peaks showed a progressive reduction to near-zero levels in Group E-500. Statistical analysis confirmed that Group E-500 showed a significant downward linear trend, $F(1, 14) = 79.19$, $p < .01$, $MSE = 0.065$, but Group Control did not, $F(1, 14) = 1.44$, $p > .10$, $MSE = 0.065$. Group E-500 also showed spontaneous recovery of early peaks between sessions. That is, the mean likelihood of an early peak in the first block of the second, third, and fourth sessions of Stage 2 was significantly higher than the likelihood in the last block of the previous session, $F(1, 14) = 9.38$, $p < .01$, $MSE = 0.055$. In contrast, Group Control continued to show early peaks at mean levels around 90% CRs (± 7%) throughout Stage 2.

In Stage 3, Group E-500 showed acquisition of CRs to CSB to a mean level of 74% CRs (± 9%), linear $F(1, 7) = 52.66$, $p < .01$, $MSE = 0.098$. Responding on A– trials showed three features. First, overall responding during A– trials appeared constant during Stage 3. Second, there was significant recovery in the likelihood of early peaks on A– trials, linear $F(1, 7) = 14.36$, $p < .01$, $MSE = 0.222$. Recovery in the early peak largely overlapped that of CR acquisition to CSB. Third, late peaks around the 500-ms point disappeared during Stage 3. Specifically, the likelihood of a CR peak during an interval 300–700 ms after CSA onset showed a significant reduction over days from a mean level of 42% CRs (± 9%) to 8% CRs (± 5%), linear $F(1, 7) = 17.84$, $p < .01$, $MSE = 0.136$.

## Discussion

The present experiment extended previous demonstrations of time-specific extinction in rabbit NM conditioning. That is, after training with a mixture of 150-ms and 500-ms ISIs, removal of the 150-ms ISI produced a progressive elimination of the early peak, punctuated by spontaneous recovery between sessions. This finding adds to the support for a time-dependent encoding of the CS. Furthermore, this finding challenges theories that view the CS as a unitary event. If the CS were encoded as a unitary event, then extinction should not have occurred, because the continued CS–US pairings at the 500-ms ISI precluded any reduction in overall CS–US associative strength, CS processing, or US processing

(e.g., Lubow, Weiner, & Schnur, 1981; Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Heth, 1975).

The evidence of time-specific extinction also challenges theories that rely on changes in context (Bouton, 2004; Capaldi, 1994). The continued presence of the US in the same number and density throughout Stages 1 and 2 eliminated the chief source of contextual change in conventional, CS-alone extinction. To use the changed ISI pattern as a new context, researchers would need a high-level learning mechanism to extract the original pattern, store it as context, extract the new pattern, and store this new pattern as a distinctive context. Such a change in the stored context could only have occurred slowly in Stage 2 as the change in the ISI pattern accumulated over trials. Accordingly, extinction of the early peak should have occurred slowly relative to conventional extinction. In fact, the early peak entirely disappeared after 4 days of Stage 2 training in Group E-500. Likewise, in conventional extinction using similar parameters, CRs also disappeared entirely within four to five sessions (Macrae & Kehoe, 1999; Napier et al., 1992).

In addition to extending previous demonstrations of time-specific extinction, concurrent recovery of the early peak to CSA during CSB–US training was demonstrated. This recovery was specific to the 150-ms point because the CR peak at the 500-ms point during CSA disappeared during Stage 3. This recovery of one peak and extinction of another peak is contrary to context-based theories of extinction. Although the construct of context is highly malleable, it would be tightly circular to argue that training with a distinctive CSB causes a highly localized change from a context of extinction to a context of learning at the 150-ms point in CSA while allowing the reverse change to occur at the 500-ms point.

In conclusion, these results generally support time-based models of conditioning. Just as CR acquisition depends on the ISI, CR elimination occurs whenever there is a change in ISI. From this perspective, conventional CS-alone extinction is an instance in which the ISI becomes infinitely long (Gallistel & Gibbon, 2000). Thus, a change in the timing requirements appears to be the necessary and sufficient condition for the down-regulation of a CR. However, this conclusion does not imply that contextual variables make no contribution to CR expression. Indeed, they have considerable influence in the rabbit NM preparation as well as in other species and response systems (Giftakis & Tait, 1998; Hinson, 1982; Kehoe, Weidemann, & Dartnall, 2004; Kim, 1986; Penick & Solomon, 1991; Poulos, Pakaprot, Mahdi, Kehoe, & Thompson, 2006; Saladin & Tait, 1986).

The present results are purely behavioral and by themselves cannot definitely point to any specific neural mechanism. Nevertheless, they are consistent with cerebellar models of NM conditioning. Both ISIs, especially the 150-ms ISI, appear too short to allow a prominent contribution from extracerebellar structures (Beylin et al., 2001; Moyer, Deyo, & Disterhoft, 1990). As described in the introduction, the architecture of the cerebellar cortex appears appropriate for time-specific acquisition and extinction. Moreover, with respect to concurrent recovery and other cross-modal effects seen in rabbit NM conditioning (Kehoe, 1988; Kehoe & Napier, 1991b; Macrae & Kehoe, 1999), the cerebellar cortex seems to have at least part of the necessary apparatus. Each Purkinje cell receives a large number of inputs from the granule cells that encode different sensory inputs. At present, however, it is uncertain how granule-Purkinje synapses modified by CSA–US pairings would be reactivated through a different set of granule-Purkinje synapses modified by CSB–US pairings. Alternatively, there are other points of polysensory convergence in the sensory inputs to the cerebellum that may produce the sensory cross-talk needed for concurrent recovery (Bao, Chen, & Thompson, 2000; Davis & Young, 1997; Tracy, Thompson, Krupa, & Thompson, 1998).

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Received December 18, 2006
Revision received March 14, 2007
Accepted April 20, 2007 ■