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Strike-induced chemosensory searching (SICS) in Northern Pacific Rattlesnakes *Crotalus viridis oreganus* HOLBROOK, 1840, rescued from abusive husbandry conditions
(Squamata: Serpentes: Viperidae)

Veränderungen im chemosensorischen Beutesuchverhalten nach dem Beutebiß (SICS) bei Nordpazifischen Klapperschlangen, *Crotalus viridis oreganus* HOLBROOK, 1840, nach inadäquater Haltung
(Squamata: Serpentes: Viperidae)

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KURZFASSUNG

Sechs Nordpazifische Klapperschlangen (*Crotalus viridis oreganus* HOLBROOK, 1840), die in privater Hand unter sehr schlechten Bedingungen gehalten worden waren, gelangten nach Woodland Park Zoological Gardens (Seattle, WA) und wurden kurz danach an die Universität von Colorado verbracht. Die Schlangen wurden innerhalb eines Monats nach ihrer Ankunft in der Universität hinsichtlich ihres chemosensorischen Beutesuchverhaltens nach dem Beutebiß (SICS) untersucht. Dabei wurden stark verminderte Züngelfrequenzen im Vergleich zu Daten von lege artis gehaltenen Klapperschlangen festgestellt. Ein Jahr nach dieser Untersuchung wurden die Züngelfrequenzen neuerlich ermittelt und lagen nun signifikant höher als während der ersten Testperiode, jedoch noch immer deutlich niedriger als dies 'normalerweise' der Fall ist. Die Untersuchungen legen nahe, daß sich das abnorme Verhalten unter guten Pflegebedingungen wieder normalisiert, daß dieser Erholungsprozeß aber Jahre und nicht etwa Wochen oder Monate in Anspruch nimmt.

ABSTRACT

Six Northern Pacific Rattlesnakes *Crotalus viridis oreganus* HOLBROOK, 1840, known to have experienced poor and abusive husbandry were acquired by Woodland Park Zoological Gardens (Seattle, WA) and shipped to the University of Colorado soon after. The snakes were tested for their tongue flicking frequency in the scope of strike-induced chemosensory searching (SICS) within one month of arrival at the University of Colorado and exhibited very low frequency values by comparison with data from rattlesnakes kept under state-of-the-art husbandry conditions. One year later tongue flicking frequency was again measured and it was significantly higher than during the first test, but still well below 'normal'. Hence, this behavior appeared to recover when the snakes were exposed to good husbandry conditions, but years, not weeks or months, may be required for full recovery.

KEY WORDS

Crotalus viridis oreganus; feeding behavior, physiology, strike-induced chemosensory searching (SICS) tongue flicking frequency, husbandry, abuse

INTRODUCTION

Rattlesnakes usually release adult rodents immediately after striking, presumably to avoid injury from struggling prey (KARDONG 1986). While this strategy reduces risk of injury to the predator, it allows the prey to wander away from the site of attack until succumbing to venom. As rodents move a considerable distance before becoming immobile, the snake's task of relocating the prey can be formidable (BROCK 1980; ESTEP & al. 1981; HAYES & GALUSHA 1984). Striking is followed by a high rate of tongue flicking coupled with searching movements, collectively called strike-induced chemosensory searching (SICS), which facilitates location and following of the prey's trail (CHISZAR & al. 1977; see HALPERN 1992 for a review of this and related topics in reptile chemoreception). Studies of SICS have demonstrated the behavior to occur in numerous venomous species with similar behaviors occurring in nonvenomous snakes and in some lizards (COOPER 1989, 1994; COOPER & al. 1989; BOYER & al., 1995). Newborn rattlesnakes exhibited SICS and trail following during their first feeding experience, and the behavior was as effective then as it was after 10 feeding episodes (GRAVES & al. 1987; SCUDDER & al. 1992). Rattlesnakes raised in captivity and fed entirely on dead prey exhibited normal SICS when the snakes were offered live prey requiring envenomating strikes (O'CONNELL & al. 1982; CHISZAR & al. 1985). Consequently, SICS appears to be a widespread, innate modal action pattern, functional at birth, and robust in the sense of resisting the degenerative effects of disuse and also in the sense of resisting various potentially disruptive stimuli (e. g., O'CONNELL & al. 1981). However, all of these studies were done with apparently healthy snakes kept under state-of-the-art husbandry conditions. It is of interest, therefore, to assess SICS in snakes that have been compromised by poor husbandry, as such animals could provide a test of the robustness of the phenomenon.

MATERIALS AND METHODS

Subjects

An opportunity arose when six abused Northern Pacific rattlesnakes *Crotalus viridis oreganus* HOLBROOK, 1840 were acquired by the Woodland Park Zoological Gardens (WPZG) in the Summer of 1994 and shipped to the University of Colorado in December of that year. The 'Animal Data Transfer Form' accompanying the shipment contained these comments: 'Had been very neglected by a private person who had them in his collection, then left town and left the snakes in the care of someone disinclined to actually work with them'. Other notes indicated that the snakes were underweight, reflecting the poor husbandry experienced before their arrival. At WPZG the snakes were maintained in separate cages to facilitate veterinary observations and monitoring of food intake. Several rodent (*Mus musculus*) meals were consumed by each snake before shipment to the University of Colorado with all appropriate paperwork (State of Washington, Department of Fish and Wildlife; U. S. Department of Agriculture, Animal and Plant Health Inspection Service; and American Association of Zoo Veterinarians Standard Certificate of Veterinary Inspection).

Upon arrival at the laboratory (12/8/94), snakes were maintained individually in glass terraria (32 cm x 61.5 cm x 31 cm) with paper floor covers and stainless steel vessels filled with water. Laboratory temperature (26°C) and photoperiod (12 hr light, 12 hr dark, lights on at 0700) were controlled by solid state switching devices. *Mus musculus* were offered on 12/14/94, with three snakes accepting and three refusing. By 1/31/95 all snakes had accepted at least one mouse, and our SICS study was initiated in February, 1995. A second SICS study was initiated in January, 1996, to determine if behavioral change occurred during one year in captivity under good husbandry conditions. The average weight of the snakes upon arrival at WPZG was 209 g, at least 100 g underweight (KLAUBER 1937). Their average weight after completion of the present experiment was 377 g, revealing the apparent consequences of time spent under proper husbandry conditions.

Method

Fundamentals of the procedures used are explained in depth in CHISZAR & al. (1992). A snake was observed for 10 minutes, during which the number of tongue flicks was recorded minute by minute on hand-held counters. We regard these counts as reflecting baseline rate of tongue flicking. Next, the snake was presented with a mouse suspended from tongs just outside of striking range (about 10-15 cm from the snake's head) for three seconds. The mouse was then removed, and the number of tongue flicks was recorded minute by minute for 30 minutes (post

Table 1: 'Giving Up Time': Average number of minutes until zero tongue flicks are emitted after 'No-Strike' (NS, n=6) and 'Strike' (S, n=6) presentations. (SE) - Standard error.

Tab.1: 'Aufgabezeit' ('Giving Up Time'): Mittlere Dauer (in Minuten) bis zum Absinken der Züngelfrequenz auf Null nach Beutetierdarreichungen ohne Biß (NS, n=6) und mit Biß (S, n=6). (SE) - Standardfehler, Range - Spannweite.

Test period Testperiode	NS	(SE)	Range	S	(SE)	Range
I (Feb. '95)	2.0	(0.6)	1-5	8.3	(2.3)	3-13
II (Jan. '96)	3.5	(1.5)	1-11	18.3	(3.4)	5-30

presentation period). Data from this no-strike (NS) condition were compared with data following an identical presentation, except that the mouse was brought closer to the snake so that a strike was permitted [strike (S) condition]. The envenomated prey was removed immediately after being released by the snake, and the number of tongue flicks was again recorded minute by minute for 30 minutes (post presentation period). Three snakes received NS trials first and S trials one week later, while the remaining three snakes received the reverse order of presentation. Identical procedures were followed in the February 1995 and January 1996 experiments.

Reliability of tongue flick counts has been assessed by having two observers independently record data from the same snake at the same time. Correlations between minute-by-minute records of independent observers have always been above 0.90 (CHISZAR & al. 1991 and references therein). When the first and second authors of the present paper made simultaneous observations of a rattlesnake in an S condition, the correlation between their minute-by-minute records was 0.96 (df = 38, p < 0.01, n = 6), indicating strong reliability.

RESULTS

Mean rates of tongue flicking in both test periods are shown in figure 1. Baseline rates were always low, indicating that snakes were quiescent prior to NS and S presentations and that the presence of the observer did not have an arousing effect on this dependent variable.

Tongue flicking rates following NS presentations exhibited a slight elevation above baseline, but only during the first 10 minutes. Thereafter the NS rates of tongue flicking remained at baseline (i. e., zero). The S conditions were quite different, however. During both test periods, significantly higher rates of tongue flicking were seen after S than after NS presentations (F = 22.60, df = 1,5, p < 0.05, n = 6). Tests after ANOVA revealed that this was true within test period I (F = 12.82, df = 1,5, p < 0.05, n = 6) as well as within test period II (F = 49.68, df = 1,5, p < 0.05, n = 6). As implied by these two F ratios and by figure 1, the magnitude of SICS effect was larger during test period II than during test period I, especially during the first 15 minutes of the post-presentation period. This gave rise to a significant interaction among (minutes x NS) versus (S x number of test period) (F = 1.75, df = 29,145, p < 0.05, n = 6). That is, the initial rate of toungue flicking after S presentations was higher than after NS presentations, and this difference was greater during test period I than during test period II.

Another view of the change in performance between the test periods can be seen by looking at 'giving up time', operationally defined as the number of minutes elapsing after NS and S presentations until zero tongue flicks are emitted (table 1). In both test periods the snakes quit tongue flicking quickly after NS presentations.

The 'giving up time' after S presentations was significantly longer than after NS presentations (F = 26.26, df = 1,5, p < 0.05, n = 6). Most interestingly, the difference between the two S presentations was significant (F = 6.85, df = 1,5, p < 0.05, n = 6), indicting that 'giving up time' was longer in test period II than in test period I. That is, the snakes exhibited more tongue flicking and greater persistence during the second test than during the first.

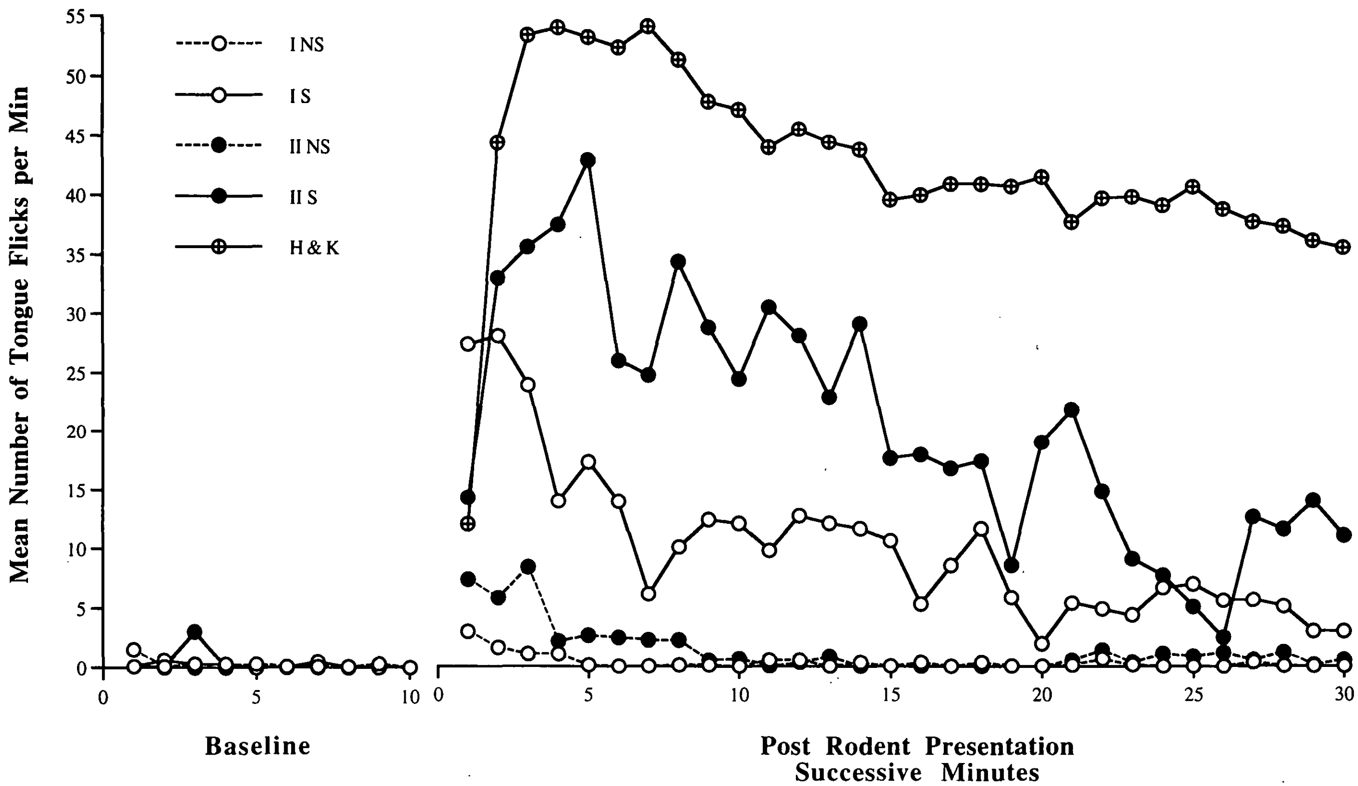

Fig. 1: Mean rate of tongue flicks per minute during baseline periods ($n=6$) and after No Strike (NS) and Strike (S) presentations of prey in *Crotalus viridis oreganus* HOLBROOK, 1840, rescued from abusive husbandry conditions. ○ - Test period I [February 1995] (I NS, I S, $n=6$); ● - Test period II [January 1996] (II NS, II S, $n=6$); ⊕ - data from HAVERLY and KARDONG (H & K) obtained with long-term, well-acclimated captive *C. v. oreganus* ($n=6$), representing what we consider the 'normal' level of SICS performance expected from well treated rattlesnakes.

Abb. 1: Mittlere Anzahl von Züngelbewegungen pro Minute (Ordinate) bei zuvor schlecht gehaltenen *Crotalus viridis oreganus* HOLBROOK, 1840, in der 'Grundfrequenz' (baseline, $n=6$) sowie während der ersten 30 Minuten nach Beutedarreichung 'ohne Biß' (NS) und 'mit Biß' (S). ○ - Testperiode I [Februar 1995] (I NS, I S, $n=6$); ● - Testperiode II [Jänner 1996] (II NS, II S, $n=6$); ⊕ - Daten nach HAVERLY & KARDONG (H & K) von gut akklimatisierten, langzeit-gefangengehaltenen *C. v. oreganus*, ($n=6$), welche die als 'normal' anzusehende Züngelfrequenz adäquat gehaltener Klaperschlangen repräsentieren.

DISCUSSION

Previous work has shown that apparently healthy rattlesnakes maintained under good husbandry conditions exhibit strong SICS on their first test and continue to do so, unchanged, on subsequent tests (e. g., SCUDDER & al. 1992). Clearly, however, the post-strike behavior of the present rattlesnakes changed between the two test periods, indicating that some recovery of function occurred, presumably as a consequence of receiving good husbandry during the interim. Two points should be made about this transformation. First, because we lack a control group of comparable snakes that continued to suffer neglect, we cannot be certain that the change observed between test periods I and II is a function of our husbandry conditions. It is possible (though unlikely) that such changes would have occurred in the controls. Second, because we lack a group of *C. v. oreganus* that has always received excellent captive treatment, we cannot be certain of the level of performance such well-acclimated animals would exhibit in our tests. However, data provided to us by HAVERLY & KARDONG (personal communication and 1996) arose from procedures very similar to those used in the present study, and the *C. v. oreganus* in their study were all long-term, well-acclimated captives, representative of snakes receiving excellent husbandry. The data of HAVERLY & KARDONG are shown in figure 1, where it is clear that tongue flicking performance of these animals was well beyond the level shown during our second replication. Hence, we must recognize that although some recovery of function has occurred in the present snakes, they are nevertheless still far from what we consider 'normal'. This leads to two considerations that may be of general interest to herpetologists:

(1) poor husbandry can have drastic effects on the behavior of snakes even though the animals exhibit no obvious morphological abnormalities except for low body weight; and

(2) recovery from these effects can require a very long time, years rather than weeks or months.

Mechanisms mediating such prolonged effects are unclear and may involve a combination of those discussed by BURGHARDT (1977) and those discussed by various authors in the volume by WARWICK & al. (1995). These papers summarize the various forms of learning and other effects of experience, especially stressful experience, that are known to occur in reptiles. We agree with GUILLETTE & al. (1995) who argued that information of practical and theoretical value may arise from studies of the exposure of reptiles to chronic stressors and of the recovery of these animals from the effects of such stressors.

While the previous assertions are speculative, we can end this paper on a relatively firm statement. Even though the behavior of the present snakes probably reflects their unfortunate early experience, SICS was present in test period I (albeit in subdued form), attesting to the fair robustness of this phenomenon. Hence, SICS survives not only the degenerative effects of disuse, but also the (presumably stronger) effects of neglect and mistreatment. We will continue to monitor the behavior of these *C. v. oreganus*, expecting that full recovery of SICS will be present by the end of two years of maintenance under good husbandry conditions (or that evidence will arise that poor husbandry may have permanent depressing effects on feeding behavior).

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