

Cross-modal effects on learning: a seismic stimulus improves color discrimination learning in a jumping spider

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Summary

The production of multimodal signals during animal displays is extremely common, and the function of such complex signaling has received much attention. Currently, the most frequently explored hypotheses regarding the evolution and function of complex signaling focus on the signal and/or signaler, or the signaling environment, while much less attention has been placed on the receivers. However, recent studies using vertebrates suggest that receiver psychology (e.g. learning and memory) may play a large role in the evolution of complex signaling. To date, the influence of multimodal cues on receiver learning and/or memory has not been studied in invertebrates. Here, we test the hypothesis that the presence of a seismic (vibratory) stimulus improves color discrimination learning in the jumping spider *Habronattus dossenus*. Using

a heat-aversion learning experiment, we found evidence for a cross-modal effect on color learning. Over a series of training trials, individuals exposed to a seismic stimulus jumped onto the heated color less frequently and remained there for less time than did individuals not exposed to a seismic stimulus. In addition, in a final no-heat test trial, individuals from the seismic-present treatment were more likely to avoid the previously heated color than were individuals from the seismic-absent treatment. This is the first study to demonstrate a cross-modal influence on learning in an invertebrate.

Key words: avoidance learning, cross-modal interactions, jumping spider, multimodal, receiver psychology, seismic signal.

Introduction

Many animals incorporate multiple signals, either within or across sensory modalities, into a single display and there is growing literature on the evolution and function of complex signaling (for reviews, see Candolin, 2003; Hebets and Papaj, 2005; Partan and Marler, 2005). While a majority of empirical and theoretical work has thus far focused on testing content-based hypotheses (e.g. Johnstone, 1996; Møller and Pomiankowski, 1993), studies incorporating content-based, efficacy-based and inter-signal interaction approaches are necessary for a complete understanding of complex signal function (see Candolin, 2003; Hebets and Papaj, 2005).

Research on inter-signal interactions (i.e. instances where the presence of one signal influences a receiver's response to a second signal), particularly cross-modal effects, may be especially important for understanding how a receiver's sensory, processing and storing capabilities [i.e. 'receiver psychology' (Guilford and Dawkins, 1991)] shape ultimate signal form (Guilford and Dawkins, 1991; Rowe, 1999). For example, in humans, the detectability of sound is improved by an irrelevant light (Lovelace et al., 2003), and visual discrimination improves when tactile stimulation is also present (Spence et al., 1998). Other studies with humans have demonstrated that a prior sensory stimulus can prime the

nervous system for the perception of future sensory information (Calvert et al., 1997; Komura et al., 2005).

Similar cross-modal interactions have been documented in other vertebrate taxa (e.g. Rowe and Guilford, 1996; Rowe, 2002), but relatively little remains known about signal interactions in invertebrates. Nonetheless, some of the few documented cases of cross-modal interactions in invertebrates come from spiders. For example, the seismic courtship signal of the wolf spider *Schizocosa uetzi* has been shown to influence a female's visual attention (Hebets, 2005). Attention-priming effects are also known from the foraging behavior of salticids, with odor from a prey item priming selective visual attention to that particular prey type (Clark et al., 2000; Jackson et al., 2002).

While such studies have begun to add to our understanding of invertebrate receiver psychology, no studies to date have explored the potential influence of complex signaling on invertebrate learning and/or memory. Furthermore, the cognitive abilities of invertebrates are often underestimated compared with those of vertebrates. Recent studies have suggested that learning and memory may play a more important role in arthropod life history than previously thought (Brembs, 2003; Edwards and Jackson, 1994; Elias et al., 2006; Hebets and Vink, 2007; Hebets, 2003; Jackson and Li, 2004; Skow and

Jakob, 2006; Tibbetts and Dale, 2004). Thus, here we chose to use an invertebrate predator, the jumping spider *Habronattus dossenus*, to determine whether multimodal cues can influence learning, as has been demonstrated in several vertebrate taxa.

Jumping spiders are diurnally active and most are generalist hunters that rely heavily on visual and seismic information in both foraging and intraspecific contexts (Edwards and Jackson, 1993; Elias et al., 2005; Forster, 1982a; Forster, 1982b; Hill, 1979; Jackson and Pollard, 1996; Land, 1969a; Taylor et al., 1998). Their anterior median eyes are adapted for both high spatial resolution (Eakin and Brandenburger, 1971) and for color vision (DeVoe, 1975; Land, 1969a; Land, 1969b; Land, 1985; Peaslee and Wilson, 1989). These eyes, in combination with three pairs of motion-detecting eyes, result in the most highly developed visual system in spiders (Land, 1985). In addition to their advanced visual capabilities, jumping spiders have also been studied with respect to their cognitive capabilities. They have been shown to use a variety of cognitive skills, including complex decision-making, detour routing and opportunistic smokescreens (using environmental noise to hide stalking movements) (Edwards and Jackson, 1993; Edwards and Jackson, 1994; Jackson and Li, 2004; Tarsitano and Andrew, 1999; Tarsitano and Jackson, 1994; Wilcox and Jackson, 1998). Of particular relevance to the present study, Nakamura and Yamashita recently established that jumping spiders are able to learn a heat-avoidance task based upon colored substrates (Nakamura and Yamashita, 2000).

Here, using an avoidance learning paradigm, we test the hypothesis that multimodal cues influence learning in the jumping spider *H. dossenus*. Specifically, we test whether the presence of a seismic stimulus influences color discrimination learning. We trained female *H. dossenus* to associate a particular color with heat in the presence and absence of a seismic stimulus. *Habronattus dossenus* females were chosen because they are known to rely on seismic signals in addition to visual signals in the context of courtship (Elias et al., 2005; Elias et al., 2006). We found evidence of a cross-modal effect on learning – spiders exposed to a seismic stimulus were better able to learn the association between the color and the heated side compared with those that received no seismic stimulus.

Materials and methods

Spider maintenance

Mature female *H. dossenus* Griswold 1987 were collected in the first two weeks of May 2006 from the Atascosa Mountains in Southeastern Arizona, USA (31°25.701' N, 111°10.404' W; Coronado National Forest, Santa Cruz County, AZ, USA). Spiders were housed individually in clear 3×3×6.7 cm plastic boxes. The spiders were maintained on a 12 h:12 h light:dark cycle and were fed two to three crickets (*Acheta domesticus*; body length=0.5 cm) once every week (spider body length=1 cm). Being adapted to arid conditions, *H. dossenus* can get sufficient water from their food, so additional water was not provided.

Experimental arena

We tested the ability of female jumping spiders to associate color with heat in the presence *versus* absence of a seismic stimulus. The experimental arena consisted of two platforms

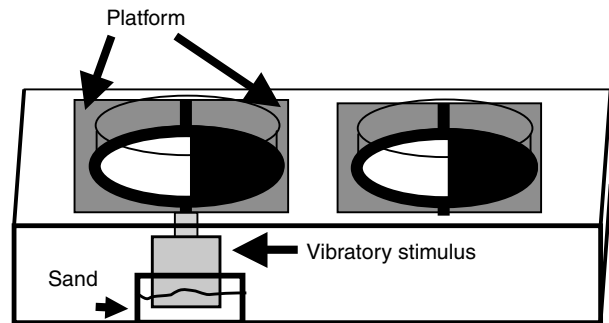


Fig. 1. Experimental arenas. Black-and-white semicircles represent yellow and red papers placed at the bottom of each arena. The papers were aligned such that one color was completely on the heated side of the aluminum platform and the other color was completely above the non-heated side of the platform. Spiders were dropped into the center of the arena where there was no heat (due to the line of epoxy).

(one seismic-present and one seismic-absent; see below), each with one side heated (Fig. 1). The bottom of each platform was constructed from two 0.125×7.5×15 cm sheets of aluminum connected with epoxy. Heat was provided by attaching a heating element underneath one side of each platform (MINCO polyamide heat element, Minneapolis, MN, USA). For the seismic-present platform, a 1 cm-diameter hole was drilled at 7.5 cm along the epoxy line between the aluminum plates. Through this hole, we attached a mini-shaker (Brüel & Kjør Type 4810, Naerum, DK) to the paper that comprised the floor of the platform. Both platforms were suspended 10 cm above the floor to enable the mini-shaker to fit below. We placed the mini-shaker in a container with 3 cm of sand to prevent vibrations from passing to the non-vibration platform (Fig. 1). One small Petri dish (diameter=8.8 cm, height=2 cm) was placed in the middle of each of the seismic-present and seismic-absent platforms, with the open side facing down to provide an enclosure for the test spiders. In order to introduce the test spiders into the enclosures, a 1 cm-diameter hole was drilled in the middle of each Petri dish. The enclosures were visually isolated from one another by a 3 cm-high border of white paper surrounding each Petri dish.

Visual stimulus

We used two visually distinct colors of construction paper, red and yellow, for the color discrimination task (BriteHue, Red and Sun Yellow, Cohoes, NY, USA). The reflectance spectra of these two colored papers are distinct and have reflectance within the visual sensitivity range of jumping spiders (Fig. 2) (Peaslee and Wilson, 1989). For each color, we cut multiple 8.5 cm-diameter semi-circles. Two semi-circles, one of each color, were placed together to make a complete circle that would ultimately provide the floor of the test enclosure. The bicolor circles were placed on the platforms underneath each Petri dish such that the junction between the colors rested on top of the epoxy line (Fig. 1). In the seismic-present arena, both pieces of paper were taped to the mini-shaker, which extended through a 1 cm-diameter hole in the center of the arena (see above). In the seismic-absent arena, the pieces of paper were both taped to the epoxy at the center of the arena. To control for luminance

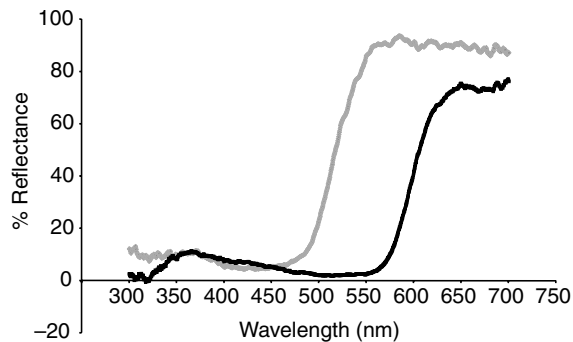


Fig. 2. Spectral reflectance profiles of yellow (gray line) and red (black line) papers used as the floor of the arenas. These have distinct reflectance signatures, which are both within the visual range of jumping spiders (Land, 1985).

variation between arenas, we used one fiber-optic light arm from the same 150 W halogen light source 10 cm above each arena, and this light source was never moved.

Seismic stimulus

For our seismic-present treatment, we used a band-limited broadband seismic stimulus (1–1500 Hz). This range was chosen based on frequencies known to be ecologically relevant for *H. dossenus* (Elias et al., 2003). The noise stimulus was created using MatLab (v.6.5.1, Natick, MA, USA). A mini-shaker was used to produce substrate vibrations in one of the experimental arenas (Brüel & Kjør Type 4810). The frequency response of the mini-shaker was flat across all tested frequencies. The seismic stimulus was broadcast over the entire colored paper substrate, and the same seismic stimulus was used in every vibration treatment. The intensity of the stimulus was set based on a series of preliminary trials where we determined the highest level of seismic stimulus that still maintained normal spider movement in the arena (based on qualitative observations).

Experimental design

Individual females were randomly assigned to either a seismic-present ($N=11$) or seismic-absent ($N=11$) treatment. Within each of these treatments, females were assigned either red or yellow as the heated color. These assignments did not change for an individual female during the course of the entire experiment. All females were initially run through an unheated control trial, which allowed us to test for any *a priori* color preferences (Gamberale-Stille and Tullberg, 2001; Rowe and Guilford, 1996). Next, females were run through 10 training trials during which heat was present. Finally, they were run through a no-heat test trial. One seismic-present and one seismic-absent treatment were run simultaneously during all trials.

Before starting each trial, we measured the temperature of both sides of each arena with a thermocouple. The seismic stimulus was then turned on and two test females were inserted into the center of their respective arenas simultaneously using a syringe with the tip removed. The seismic stimulus was on during the entirety of all trials for the seismic-present group. The center of the arena where the females were initially placed did not have heat (due to the epoxy line), but both colors were present.

As mentioned above, each female was run through an initial control trial in which neither side of the platform was heated (i.e. platform was maintained at room temperature: $23.2 \pm 1.3^\circ\text{C}$, mean \pm s.d.). During this 5 min control trial, we scored the number of times an individual ventured into each side of the arena as well as the total number of times the spider jumped. We used the number of times a spider jumped as a measure of the individual's activity level since *H. dossenus* move around primarily by stepping and jumping (N.D.V. and D.O.E., unpublished observation). Individuals that did not go onto both colors at least once were excluded from the experiment ($N=2$; one individual from the seismic-present group and one from the seismic-absent group).

For the 10 training trials, one side of each platform was heated to 60°C ($59.9 \pm 1.1^\circ\text{C}$), while the other side was maintained at 35°C ($35.4 \pm 0.8^\circ\text{C}$). In the first training trial, we dropped spiders onto the heated color to ensure that all spiders were exposed to the heat at the same time. All training trials lasted 5 min. For the training trials, we monitored the number of times an individual ventured onto the heated color, how long it spent on the heated color, and the number of times an individual jumped while on the non-heated color. Individuals often greatly increased the speed and number of jumps while on the heated color, making it difficult to accurately count; we therefore excluded these jumps from the data analysis.

All individuals ($N=10$ for each treatment group) were run through 10 consecutive training trials, with 15 min separating each trial. During the inter-trial interval we changed the colored papers, cleaned the syringe with 70% ethanol and re-measured the temperature of each side of both arenas. We also rotated the platforms clockwise 90° to control for spiders orienting to visual stimuli above the arena.

Upon completion of 10 training trials, each female was run through a 5-min no-heat test trial. This trial allowed us to determine if the spiders had learned to avoid the color that was heated, rather than just detecting the heat and avoiding the heated side. The test trials took place 20 min after the final training trial, after the platforms were cooled to room temperature ($26.2 \pm 1.2^\circ\text{C}$). Females were again introduced into the middle of the arena and we measured whether or not an individual went onto the previously heated color, the delay until an individual went onto the previously heated color, and the total number of individual jumps.

Statistical analysis

We performed four independent-samples *t*-tests to ensure that the randomly assigned heated color had no effect on overall activity levels, number of jumps onto the heated color or duration of time spent on the heated side. Individual activity levels (number of jumps) in the seismic-present and seismic-absent treatment groups were analyzed for the control trial, training trial 1 and trial 10, with independent-samples *t*-tests. Comparisons of activity levels for individuals within a treatment group between trial 1 and 10 were analyzed with paired-samples *t*-tests. The number of times an individual went onto the heated side, and the duration of time spent on the heated side in training trial 1 and trial 10 were compared between groups with independent-samples *t*-tests and within groups between trials 1 and 10 with paired-samples *t*-tests. Bonferroni-corrected

significance levels were used in all cases where multiple tests were done on the same data ($P=0.05/\text{number of tests}$). All tests were performed using SPSS (v.14.0, Chicago, IL, USA). Results of statistical tests (not including temperature averages, which are means \pm s.d.) are all reported as means \pm s.e.m.

Responses in the final test trial were analyzed in two different ways. First, the number of individuals that went onto the previously heated color was analyzed with a χ^2 test. Since all individuals were screened for potential color biases in the initial no-heat control trial, we assume that all 10 individuals in each treatment group would go onto the previously heated color during the test trial if there was no learning during the training trials. We therefore set our null hypothesis value to '10' for the χ^2 test ($N=10$ for both treatment groups). A Yates correction was used in these calculations to control for only one degree of freedom (Zar, 1998). In a second analysis, the latency to first contact of the previously heated color was analyzed using an independent-samples t -test (SPSS v.14.0). Individuals that never went onto the previously heated color in the test trial were excluded from this final analysis. In the final test trial, since there was no heat associated with the previously heated color, individuals had no incentive to continue to avoid this color. Therefore, we did not analyze the number of times entered or duration of time spent on the color that had been previously heated. Instead we considered how long it took an individual to go onto the previously heated color, if at all, to see if there was any continued avoidance of the previously heated color, even when no heat cues were available.

We performed a Shapiro-Wilk W test on all of the variables' distributions to determine whether they fit a normal distribution. To ensure that our t -test results were not affected by any non-normal distributions, we then performed a generalized linear model with quasi-Poisson distribution using R (v.2.5.0, 2007-04-23; CRAN, Vienna, Austria) for all analyses that did not pass the Shapiro-Wilk W test ($P=0.05$). In all 19 analyses that we repeated, we found the same level of significance with the original t -test and the generalized linear model. We will therefore report our statistics with the t -statistic, which is more commonly known.

Results

Heated color

There was no observed effect of the color that was heated on the overall activity level of the spiders (Yellow, $N=8$, 5.1 ± 3.2 jumps; Red, $N=12$, 6.9 ± 4.4 jumps; $t=0.98$, $P=0.339$). Color also had no effect on the number of times a spider went onto the heated color in the final training trial (Y, 0.5 ± 1.1 jumps; R, 1.1 ± 1.1 jumps; $t=1.19$, $P=0.253$), the amount of time spent on the heated color in the last training trial (Y, 1.5 ± 3.9 s; R, 11.0 ± 12.4 s; $t=2.077$, $P=0.052$, Bonferroni $P=0.0125$) or the delay to the previously heated color in the test trial (Y, 98.5 ± 88.9 s; R, 131.9 ± 133.2 s; $t=0.621$, $P=0.543$). Therefore, color was excluded from all further statistical tests.

Activity levels

There was no difference in activity levels between the seismic-present and seismic-absent treatment groups across all training trials (present, $N=10$, 7.6 ± 4.3 jumps; absent, $N=10$, 4.8 ± 3.3 jumps; $t=-1.635$, $P=0.119$). Individuals in both groups

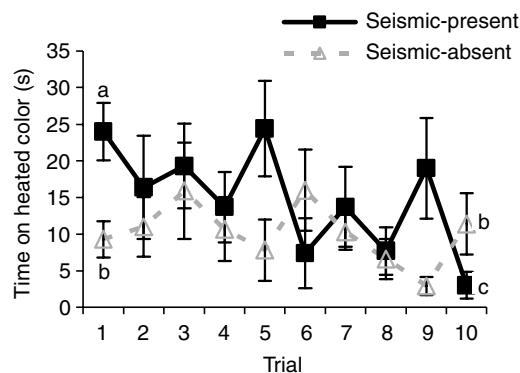


Fig. 3. Amount of time spent on heated color in the 10 training trials. Lines and error bars represent the mean and standard error. Letters indicate significant differences: a–b, $P\leq 0.025$; a–c, $P\leq 0.005$; b–c, not significant.

tended to become less active in later trials, with a greater effect seen in individuals in the seismic-present treatment (present Trial 1, 4.0 ± 2.2 jumps; Trial 10, 0.4 ± 1.0 jumps; $t=4.070$, $P=0.003$; absent Trial 1, 2.4 ± 3.1 jumps; Trial 10, 0.7 ± 0.823 jumps; $t=1.899$, $P=0.090$). However, when comparing within a trial, there was no significant difference between individuals in the seismic-present versus seismic-absent treatments (Trial 1 present, 4.0 ± 2.2 jumps; Trial 1 absent, 2.4 ± 3.1 jumps; $t=-1.329$, $P=0.200$; Trial 10 present, 0.4 ± 1.0 jumps; Trial 10 absent, 0.7 ± 0.823 jumps; $t=0.747$, $P=0.464$).

Time spent on heated color

In trial 1, individuals in the seismic-present treatment spent significantly more time on the heated color than individuals in the seismic-absent treatment (Fig. 3) (seismic-present, 24.1 ± 12.6 s; seismic-absent, 9.3 ± 7.9 s; $t=-3.148$, $P=0.006$). By the tenth trial, however, there was a trend that individuals exposed to a seismic stimulus were spending less time on the heated color than individuals without seismic exposure (Fig. 3) (seismic-present, 3.0 ± 5.7 s; seismic-absent, 11.4 ± 13.3 s; $t=1.834$, $P=0.083$). Individuals within the seismic-present treatment group spent significantly less time on the heated color in Trial 10 compared with Trial 1 (Fig. 3) (Trial 1, 24.1 ± 12.6 s; Trial 10, 3.0 ± 5.7 s; $t=4.206$, $P=0.002$), while there was no difference between Trial 1 and Trial 10 in individuals with no seismic exposure (Fig. 3) (Trial 1, 9.3 ± 7.9 s; Trial 10, 11.4 ± 13.3 s; $t=-0.625$, $P=0.548$).

Number of jumps onto heated color

Seismic-present and -absent treatment groups did not differ in the number of times individuals went onto the heated color in trial 1 (Fig. 4) (seismic-present, 2.3 ± 1.4 jumps; seismic-absent, 1.5 ± 1.1 jumps; $t=1.419$, $P=0.173$). However, in the tenth trial, individuals in the seismic-present treatment group went onto the heated color significantly fewer times than individuals without seismic exposure (Fig. 4) (seismic-present, 0.3 ± 0.5 jumps; seismic-absent, 1.4 ± 1.3 jumps; $t=-2.569$, $P=0.019$). In addition, within the seismic-present treatment there was a significant decrease in the number of times individuals went onto the heated color between Trial 1 and Trial

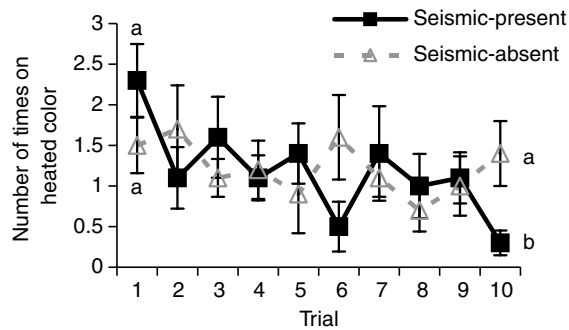


Fig. 4. Number of times individuals went onto the heated color in the 10 training trials. Lines and error bars represent the mean and standard error. Letters indicate significant differences: a–b, $P \leq 0.025$.

10 (Fig. 4) (Trial 1, 2.3 ± 1.4 jumps; Trial 10, 0.3 ± 0.5 jumps; $t = 3.873$, $P = 0.004$). By contrast, in the seismic-absent treatment, there was no difference between the number of times an individual went on the heated color in the first and the tenth trials (Fig. 4) (Trial 1, 1.5 ± 1.1 jumps; Trial 10, 1.4 ± 1.3 jumps; $t = 0.208$, $P = 0.840$).

Test trial

There was a significant difference between the seismic-present versus seismic-absent treatment groups in the number of individuals that went onto the previously heated color during the no-heat test trial (Fig. 5) (seismic-present, $N = 10$; seismic-absent, $N = 10$; $\chi^2 = 5.0$, $P = 0.025$). Of the individuals that went onto both colors, there was no difference in the latency to going onto the previously heated color (seismic-present, $N = 6$, 62.2 ± 47.3 s; seismic-absent, $N = 9$, 55.3 ± 56.0 s; $t = 0.245$, $P = 0.810$).

Discussion

This study illustrates a cross-modal effect on learning in the jumping spider *Habronattus dosseus*. Specifically, our results demonstrate that the presence of a general seismic stimulus enhances performance on a color discrimination task. We observed improved avoidance of the color associated with an aversive stimulus in the presence of a seismic stimulus both across training trials and in a final no-heat test trial. Over time, individuals in the seismic-present treatment entered the heated

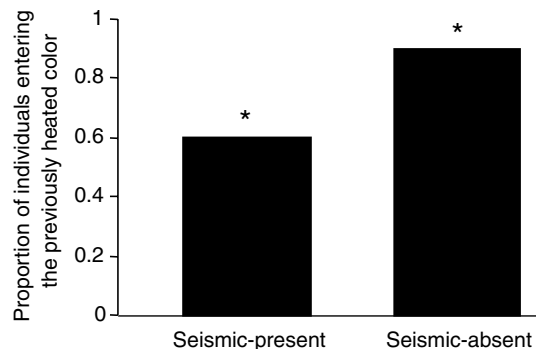


Fig. 5. Proportion of individuals that went onto the previously heated color during the test trial. Asterisks indicate significant difference ($P < 0.025$).

side fewer times than did individuals in the seismic-absent treatment. In addition, in the final no-heat test trial, seismic-present individuals were less likely to go on the previously heated color than were seismic-absent individuals, demonstrating that our observed learning differences were not simply due to a method of detecting, and then avoiding, heat.

Individuals in the seismic-present treatment initially spent more time on the heated color than did individuals in the seismic-absent treatment. However, over time, seismic-present individuals significantly decreased the amount of time spent on the heated color while no such decrease was observed in the seismic-absent treatment. Despite the initial increased time spent on the heated side by individuals in the seismic-present treatment, we found no differences in overall activity levels (as measured by number of jumps) between the seismic-present and -absent treatment groups. We argue that duration of time spent on the heated color may not be an accurate indication of learning in this type of experimental design as individuals may react differently once introduced to a heated surface, with some 'freezing' and others jumping around until they happened to land on the non-heated color. We observed both types of responses in both the seismic-present and seismic-absent treatments.

Although our statistical analyses demonstrate significant differences between the seismic-present and seismic-absent treatments, the variance across trials within a treatment group is notably high. Prior to the start of this experiment, we chose to run 10 training trials and compare the performance of the spiders in the first and last trials. Had we chosen different trial numbers for comparison, our statistical results may have differed but our general conclusions would remain the same (see Figs 3 and 4). Regardless of the specific comparisons, there was a general trend for spiders in the seismic-present group to decrease both how long they spent on the heated color and how often they went onto the heated color. No such trend was evident for the seismic-absent spiders. The most compelling evidence, however, that seismic signals enhanced color-discrimination learning came from the no-heat test trial. In this test trial, seismic-present females showed strong avoidance of the previously heated color while seismic-absent females did not. These findings are the most direct evidence of a cross-modal effect on learning.

The seismic stimulus used in this experiment conveyed no information regarding which color would be heated (i.e. the differences found across treatment groups cannot be explained as properties of the seismic stimulus alone). Instead, these differences resulted from a cross-modal interaction in which a seismic stimulus influenced some aspect of the receiver's psychology (e.g. her arousal, perception, attention or retention of visual information). This study cannot speak to the exact mechanism underlying this cross-modal interaction, but several possibilities exist. For example, the seismic stimulus may increase a female's general arousal, making her more inclined to devote attention to the association between the color and the aversive stimulus. Alternatively, the seismic stimulus may act to focus a female's visual attention (see Hebets, 2005), thus enhancing her ability to distinguish between the two colors and enabling a more accurate association between the color and the aversive stimulus. The transmission properties of the oak leaf litter substrate on which *H. dosseus* is primarily found make it

likely that the spiders are frequently exposed to environmental seismic noise (Elias et al., 2005). Consequently, the seismic-present treatment may actually mimic natural environmental conditions.

One of the more exciting implications of our results relates to our general understanding of the evolution of aposematic, or warning, coloration. For example, while the function of conspicuous warning coloration has been credited to enhance avoidance learning in predators (Cott, 1940; Endler and Greenwood, 1988; Guilford and Dawkins, 1991; Lynn, 2005), warning displays of unpalatable prey often combine aposematic coloration with signals in a secondary modality (e.g. substrate vibrations, airborne vibrations and/or chemical secretions) (Cokl and Virant-Doberlet, 2003; Cott, 1940; Poulton, 1890; Rowe and Guilford, 1999a). Recently, it has been proposed that the additional components of many warning displays may promote the association between the warning coloration and the non-profitability of the prey item for a predator (Rowe, 2002; Skelhorn and Rowe, 2006). This multimodal facet of warning displays and its interaction with predator psychology has already received much attention in studies focusing on birds (Jetz et al., 2001; Lindstrom et al., 2001; Rowe, 1999; Rowe, 2002; Rowe and Guilford, 1996; Rowe and Guilford, 1999b; Skelhorn and Rowe, 2005), yet these same ideas have not been addressed with invertebrate predators. In essence, although not previously considered, our results suggest that invertebrate predators such as jumping spiders could exert strong selection pressure on the evolution of invertebrate multimodal warning displays, many of which combine aposematic coloration with broadband vibration or sound production (Cocroft, 1996; Cocroft and Rodriguez, 2005; Hill, 2001; Masters, 1979). Due to both their abundance and the amount of prey they are capable of ingesting daily (for *H. dosseus*, up to twice their body mass daily; N.D.V., unpublished data), generalist invertebrate predators such as jumping spiders may play a much larger role than vertebrate predators in shaping insect warning displays – an area of research deserving further investigation.

In summary, the present study provides some of the first evidence of cross-modal effects on learning in an invertebrate. It offers the first demonstration that seismic stimuli can influence a color discrimination task in a jumping spider and suggests that the complicated cross-modal interactions frequently studied in vertebrate taxa are present in invertebrate groups as well. Although this study does not address the mechanism(s) underlying the observed multimodal effect on receiver psychology, a relatively ‘simpler’ invertebrate system such as jumping spiders may make such future studies more feasible.

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References

- Brembs, B.** (2003). Operant conditioning in invertebrates. *Curr. Opin. Neurobiol.* **13**, 710-717.
- Calvert, G. A., Bullmore, E. T., Brammer, M. J., Campbell, R., Williams, S. C. R., McGuire, P. K., Woodruff, P. W. R., Iverson, S. D. and David, A. S.** (1997). Activation of auditory cortex during silent lipreading. *Science* **276**, 593-596.
- Candolin, U.** (2003). The use of multiple cues in mate choice. *Biol. Rev.* **78**, 575-595.
- Clark, R. J., Jackson, R. R. and Cutler, B.** (2000). Chemical cues from ants influence predatory behavior in *Habrocestum pulex*, an ant-eating jumping spider (Araneae, Salticidae). *J. Arachnol.* **28**, 309-318.
- Cocroft, R. B.** (1996). Insect vibrational defence signals. *Nature* **382**, 679-680.
- Cocroft, R. B. and Rodriguez, R. L.** (2005). The behavioral ecology of insect vibrational communication. *BioScience* **55**, 323-334.
- Cokl, A. and Virant-Doberlet, M.** (2003). Communication with substrate-borne signals in small plant-dwelling insects. *Annu. Rev. Entomol.* **48**, 29-50.
- Cott, H. B.** (1940). *Adaptive Coloration in Animals*. London: Methuen.
- DeVoe, R. D.** (1975). Ultraviolet and green receptors in principal eyes of jumping spiders. *J. Gen. Physiol.* **66**, 193-207.
- Eakin, R. M. and Brandenburger, J. L.** (1971). Fine structure of the eyes of jumping spiders. *J. Ultrastruct. Res.* **37**, 618-663.
- Edwards, G. B. and Jackson, R. R.** (1993). Use of prey-specific predatory behavior by North-American jumping spiders (Araneae, Salticidae) of the genus *Phidippus*. *J. Zool.* **229**, 709-716.
- Edwards, G. B. and Jackson, R. R.** (1994). The role of experience in the development behavior in *Phidippus regius*, a jumping spider (Araneae: Salticidae). *N. Z. J. Zool.* **21**, 269-277.
- Elias, D. O., Mason, A. C., Maddison, W. P. and Hoy, R. R.** (2003). Seismic signals in a courting male jumping spider (Araneae: Salticidae). *J. Exp. Biol.* **206**, 4029-4039.
- Elias, D. O., Hebets, E., Hoy, R. R. and Mason, A. C.** (2005). Seismic signals are crucial for male mating success in a visual specialist jumping spider (Araneae: Salticidae). *Anim. Behav.* **69**, 931-938.
- Elias, D. O., Hebets, E. A. and Hoy, R. R.** (2006). Female preference for complex/novel signals in a spider. *Behav. Ecol.* **17**, 765-771.
- Endler, J. A. and Greenwood, J. D.** (1988). Frequency-dependent predation, crypsis, and aposematic coloration. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **319**, 505-523.
- Forster, L.** (1982a). Vision and prey-catching strategies in jumping spiders. *Am. Sci.* **70**, 165-175.
- Forster, L. M.** (1982b). Non-visual prey-capture in *Trite planiceps*, a jumping spider (Araneae, Salticidae). *J. Arachnol.* **10**, 179-183.
- Gamberale-Stille, G. and Tullberg, B. S.** (2001). Fruit or aposematic insect? Context dependent colour preferences in domestic chicks. *Proc. R. Soc. Lond. B Biol. Sci.* **268**, 2525-2529.
- Guilford, T. and Dawkins, M. S.** (1991). Receiver psychology and the evolution of animal signals. *Anim. Behav.* **42**, 1-14.
- Hebets, E. A.** (2003). Subadult experience influences adult mate choice in an arthropod: exposed female wolf spiders prefer males of a familiar phenotype. *Proc. Natl. Acad. Sci. USA* **100**, 13390-13395.
- Hebets, E. A.** (2005). Attention-altering interaction in the multimodal courtship display of the wolf spider *Schizocosa uetzi*. *Behav. Ecol.* **16**, 75-82.
- Hebets, E. A. and Papaj, D. R.** (2005). Complex signal function: developing a framework of testable hypotheses. *Behav. Ecol. Sociobiol.* **57**, 197-214.
- Hebets, E. A. and Vink, C.** (2007). Experience leads to preference in a population of syntopic wolf spiders. *Behav. Ecol.* doi: 10.1093/behaveco/arm070.
- Hill, D. E.** (1979). Orientation by jumping spiders of the genus *Phidippus* (Araneae: Salticidae) during the pursuit of prey. *Behav. Ecol. Sociobiol.* **5**, 301-322.
- Hill, P. S. M.** (2001). Vibration and animal communication: a review. *Am. Zool.* **41**, 1135-1142.
- Jackson, R. R. and Li, D.** (2004). One-encounter search image formation by araneophagic spiders. *Anim. Cogn.* **7**, 247-254.
- Jackson, R. R. and Pollard, S. D.** (1996). Predatory behavior of jumping spiders. *Annu. Rev. Entomol.* **41**, 287-308.
- Jackson, R. R., Clark, R. J. and Harland, D. P.** (2002). Behavioural and cognitive influences of kairomones on an araneophagic jumping spider. *Behaviour* **139**, 749-775.
- Jetz, W., Rowe, C. and Guilford, T.** (2001). Non-warning odors trigger innate color aversions – as long as they are novel. *Behav. Ecol.* **12**, 134-139.
- Johnstone, R. A.** (1996). Multiple displays in animal communication: ‘backup signals’ and ‘multiple messages’. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **351**, 329-338.
- Komura, Y., Tamura, R., Uwano, T., Nishijo, H. and Ono, T.** (2005).

- Auditory thalamus integrates visual inputs into behavioral gains. *Nat. Neurosci.* **8**, 1203-1209.
- Land, M. F.** (1969a). Movements of retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. *J. Exp. Biol.* **51**, 471-493.
- Land, M. F.** (1969b). Structure of the retinae of the principle eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. *J. Exp. Biol.* **51**, 443-470.
- Land, M. F.** (1985). The morphology and optics of spider eyes. In *Neurobiology of Arachnids* (ed. F. G. Barth), pp. 53-78. New York: Springer-Verlag.
- Lindstrom, L., Rowe, C. and Guilford, T.** (2001). Pyrazine odour makes visually conspicuous prey aversive. *Proc. R. Soc. Lond. B Biol. Sci.* **268**, 159-162.
- Lovelace, C. T., Stein, B. E. and Wallace, M. T.** (2003). An irrelevant light enhances auditory detection in humans: a psychophysical analysis of multisensory integration in stimulus detection. *Cogn. Brain Res.* **17**, 447-453.
- Lynn, S. K.** (2005). Learning to avoid aposematic prey. *Anim. Behav.* **70**, 1221-1226.
- Masters, W.** (1979). Insect disturbance stridulation – its defensive role. *Behav. Ecol. Sociobiol.* **5**, 187-200.
- Møller, A. P. and Pomiankowski, A.** (1993). Why have birds got multiple sexual ornaments. *Behav. Ecol. Sociobiol.* **32**, 167-176.
- Nakamura, T. and Yamashita, S.** (2000). Learning and discrimination of colored papers in jumping spiders (Araneae, Salticidae). *J. Comp. Physiol.* **186**, 897-901.
- Partan, S. R. and Marler, P.** (2005). Issues in the classification of multimodal communication signals. *Am. Nat.* **166**, 231-245.
- Peaslee, A. G. and Wilson, G.** (1989). Spectral sensitivity in jumping spiders (Araneae, Salticidae). *J. Comp. Physiol. A* **164**, 359-363.
- Poulton, E. B.** (1890). *The Colours of Animals: Their Meaning and Use, Especially Considered in the Case of Insects*. London: K. Paul, Trench, Trubner.
- Rowe, C.** (1999). Receiver psychology and the evolution of multicomponent signals. *Anim. Behav.* **58**, 921-931.
- Rowe, C.** (2002). Sound improves visual discrimination learning in avian predators. *Proc. R. Soc. Lond. B Biol. Sci.* **269**, 1353-1357.
- Rowe, C. and Guilford, T.** (1996). Hidden colour aversions in domestic chicks triggered by pyrazine odours of insect warning displays. *Nature* **383**, 520-522.
- Rowe, C. and Guilford, T.** (1999a). The evolution of multimodal warning displays. *Evol. Ecol.* **13**, 655-671.
- Rowe, C. and Guilford, T.** (1999b). Novelty effects in a multimodal warning signal. *Anim. Behav.* **57**, 341-346.
- Skelhorn, J. and Rowe, C.** (2005). Prey palatability influences predator learning and memory. *Anim. Behav.* **71**, 1111-1118.
- Skelhorn, J. and Rowe, C.** (2006). Predator avoidance learning of prey with secreted or stored defences and the evolution of insect defences. *Anim. Behav.* **72**, 827-834.
- Skow, C. D. and Jakob, E. M.** (2006). Jumping spiders attend to context during learned avoidance of aposematic prey. *Behav. Ecol.* **17**, 34-40.
- Spence, C., Nicholls, M. E. R., Gillespie, N. and Driver, J.** (1998). Cross-modal links in exogenous covert spatial orienting between touch, audition, and vision. *Percept. Psychophys.* **60**, 544-557.
- Tarsitano, M. S. and Andrew, R.** (1999). Scanning and route selection in the jumping spider *Portia labiata*. *Anim. Behav.* **58**, 255-265.
- Tarsitano, M. S. and Jackson, R. R.** (1994). Jumping spiders make predatory detours requiring movement away from prey. *Behaviour* **131**, 65-73.
- Taylor, P. W., Jackson, R. R. and Robertson, M. W.** (1998). A case of blind spider's buff? Prey-capture by jumping spiders (Araneae, Salticidae) in the absence of visual cues. *J. Arachmol.* **26**, 369-381.
- Tibbetts, E. A. and Dale, J.** (2004). A socially enforced signal of quality in a paper wasp. *Nature* **432**, 218-221.
- Wilcox, R. S. and Jackson, R. R.** (1998). Cognitive abilities of araneophagic jumping spiders. In *Animal Cognition in Nature* (ed. R. P. Balda, I. M. Pepperberg and A. C. Kamil). San Diego: Academic Press.
- Zar, J. H.** (1998). *Biostatistical Analysis*. Upper Saddle River, NJ: Prentice-Hall.