

Multimodal mixed messages: the use of multiple cues allows greater accuracy in social recognition and predator detection decisions in the mosquitofish, *Gambusia holbrooki*

Ashley J.W. Ward^a and Thomas Mehner^b

^aSchool of Biological Sciences, University of Sydney, Sydney, New South Wales 2006, Australia and

^bLeibniz-Institute of Freshwater Ecology and Inland Fisheries, 12587 Berlin, Germany

Information gathered by animals through different sensory modalities at any given point may be aligned, that is, consistent across different senses, or in conflict, where different senses provide different information. This latter instance may occur for a variety of reasons, including differences in speed of dispersal and persistence of some cues relative to others. By gathering information using multiple sensory modalities simultaneously, animals may be able to mediate this conflict and increase decision accuracy. This study examined the use of different sensory modalities over a short spatial range by mosquitofish in locating conspecifics and avoiding a cryptic sympatric predator. Fish were provided with visual and/or chemical cues either separately or simultaneously. Where visual and chemical cues were provided simultaneously, they were either aligned or in conflict. As expected, fish with access to aligned cues generally performed best, approaching a conspecific shoal sooner and spending longer in proximity to the shoal and avoiding approaching the predators for longer and spending less time in proximity to them. Fish with access to conflicting cues performed as well as those with access to aligned cues in overall time spent in proximity to predators, while they were more wary of conspecific visual cues presented in association with predator chemical cues. However, fish with access to conflicting cues were slower to approach conspecific visual cues and, crucially, faster to approach predator visual cues than fish with access to aligned cues. This suggests that although multimodal cue use generally promotes accuracy, the potential remains for conflicting cues to generate risky decisions. *Key words*: chemosense, decision-making, fish, olfaction, shoaling, vision. [*Behav Ecol* 21:1315–1320 (2010)]

Animals gather information about their environment through a range of sensory channels. By using multiple sensory channels simultaneously, animals can gather not only a greater range of information but can potentially cross-reference the different sensory information inputs to maximize accuracy (Johnstone 1996). However, because the various sensory channels operate at different spatial and temporal scales, an individual moving around in its environment will likely detect information—via some sensory cue—initially through a single sensory modality. If the individual opts to investigate, the amount of sensory information will likely increase as it homes in on the cue source, both because the initial sensory inputs may become stronger as the source is approached and also because below a certain threshold distance, new sensory channels will become operative. The new information gathered can then be used to update and inform a subsequent behavioral decision. Any new information that is found may fall into 1 of 2 categories: it may reinforce that contained by the initial cues or it may appear to conflict with the initial cues. There are many reasons why this might be the case, including signaler attempts to induce a receiver to behave in a way that benefits the signaler, such as crypsis, mimicry, and deceit (Wiley 1983; Barbero et al. 2009) or through decay of the temporal and spatial resolution and

accuracy of the information. Comparative to other sensory cues, chemical cues are often detectable over a wide range, hence the initial detection of a cue source is often through chemical cues. However, chemicals spread far more slowly and also persist in an area for longer than light and pressure (Giske et al. 1998). This could mean, for example, that chemical information about a predator will remain for a duration in a given place, after the animal itself has left the area. As a result, chemical cues can occasionally contain outdated or inaccurate information (Brown 2003), which may sometimes conflict with the information provided by other senses.

Despite this, the use of chemical cues is widespread throughout the animal kingdom (Wyatt 2003). In aquatic systems, chemical cues are of particular importance both because water acts as an excellent medium to carry a wide range of chemicals and because in many instances, visual cues are disrupted by light attenuation, turbidity, and/or habitat complexity (Giske et al. 1998). Many fishes rely heavily on chemical cues for foraging (Webster, Atton, et al. 2007), assessment of competitors (Barata et al. 2007), mate choice (Aeschlimann et al. 2003), and migration (Hasler and Cooper 1976). Detection of alarm pheromones and predation threats is also mediated extensively by chemical cues in fishes (e.g., Wisenden 2000). Furthermore, chemical cues are crucial in mediating many of the most important social interactions between shoaling fish (Ward et al. 2007; Webster, Goldsmith, et al. 2007). In a study of 2 freshwater fish species, Ward et al. (2002) determined that chemical cues were relatively more important than visual cues in species recognition.

Address correspondence to A.J.W. Ward. E-mail: ashleyjward@gmail.com.

Received 3 June 2010; revised 23 August 2010; accepted 23 August 2010.

© The Author 2010. Published by Oxford University Press on behalf of the International Society for Behavioral Ecology. All rights reserved. For permissions, please e-mail: journals.permissions@oxfordjournals.org

Herbert-Read et al. (2010) report the value of chemical cues to a social fish species in locating conspecifics at distances of greater than 20 body lengths. As it approaches a cue source, in this case a shoal of conspecifics, a searching animal should be able to augment the chemical information with input from additional sensory modalities, particularly visual cues. Although visual cues typically provide a greater amount of information than other cues, their use by fishes in shallow freshwater is constrained both by environmental factors, such as levels of light and turbidity. Furthermore, the maximum visual range of many small benthic fishes seldom extends beyond a few body lengths (Aksnes and Utne 1997; Utne-Palm 2002), hence the ability to use vision and chemosense simultaneously to cross-reference cues and thereby to gain accurate information is spatially limited.

In their natural environment, prey and their predators often live in remarkably close proximity. For example, Pitcher (1980) estimated that roach (*Rutilus rutilus*) spend a large proportion of their lives within striking distance of their predators, pike (*Esox lucius*), whereas Seghers (1974) made a similar observation in the predator-prey system of pike cichlids (*Crenicichla* spp.) and guppies (*Poecilia reticulata*). This is also the case with mosquitofish (*Gambusia holbrooki*), a species which forms loose shoals and that lives in close proximity to one of its key predators, the flathead gudgeon (*Philypnodon grandiceps*). Gudgeon are ambush predators and are not territorial, other than when a male is guarding a clutch of eggs, hence they move around their environment and launch attacks from a range of concealed positions (Ward AJW, personal observation). In order to minimize their risk from predators and to maintain close contacts with conspecifics, mosquitofish should gather information continually through the sensory modalities at their disposal. Little is known about whether, and how, animals prioritize information from different sensory modalities in these contexts. Cue conflict studies offer an insight into this process, enabling the examination of the relative importance of different sensory inputs and the question of how animals resolve conflict when it arises (Uetz and Roberts 2002).

The study examined the use of different sensory modalities over a short spatial range by mosquitofish in locating conspecifics and avoiding a sympatric predator. Most importantly, we examined how the fish respond to conflict in the sensory information that they receive. Specifically, we tested 2 main hypotheses. First, that fish provided with aligned multimodal cues would approach a shoal of conspecifics more quickly, and would spend longer in the proximity of that shoal, than fish provided with conflicting multimodal cues. Second, that fish provided with aligned multimodal cues would be slower to approach a group of predatory fish, and would spend less time in the proximity of the predators, than fish provided with conflicting multimodal cues.

MATERIALS AND METHODS

Experimental animals

Mosquitofish (*G. holbrooki*) measuring 26.9 ± 2.8 mm (mean \pm standard deviation) were collected for use in the experiments in November and December 2009 from Manley Dam, Balgowlah, Australia ($33^{\circ}46'35.45''$ S, $151^{\circ}14'50.38''$ E). Prior to experiments, mosquitofish were held for 2 weeks in three 180 l-vats in a temperature controlled room at the University of Sydney that maintained a temperature of 23.1 ± 1 °C. Flathead gudgeon (*P. grandiceps*) measuring 69.2 ± 6.2 mm (mean \pm standard deviation) were collected in October 2009 from Manly Dam and from Middle Creek, Narrabeen, Australia ($33^{\circ}43'4.79''$ S, $151^{\circ}16'25.87''$ E). Prior to experiments,

flathead gudgeon were held in one of three 90-l aquaria held in the same temperature controlled room.

Experimental apparatus and protocol

A glass tank (the experimental tank) measuring $50 \times 12 \times 15$ cm ($l \times w \times d$) was filled with aged, conditioned water to a depth of 10 cm. Lines drawn on the glass of the experimental tank divided it into 3 separate zones along its longest axis. These were a central zone of 30 cm width flanked by 2 outer zones, each 10 cm in width. At either end of this tank were placed 2 smaller glass tanks ("the visual stimulus tanks," each measuring $30 \times 14 \times 15$ cm ($l \times w \times d$) and also filled to a depth of 10 cm. The visual stimulus tanks were used to house fish that would provide visual cues to the focal fish in the experimental tank. The visual stimulus tanks were divided in half using white plastic so that the stimulus fish would be confined to the half nearest the experimental tank. Stimulus fish were provided with a sand substrate and an artificial plant for cover. Three further tanks (the chemical stimulus tanks) were set up to house stimulus fish that would provide chemical cues to the focal fish. A single 4-mm diameter tube with an in-line valve connected each of these tanks to the experimental tank. These tubes entered the experimental tank at either end. When the valves were turned on, each tube delivered water at the rate of 92 ± 7 ml/min.

A total of 40 mosquitofish were maintained in one of the chemical stimulus tanks, 10 flathead gudgeon were maintained in a second chemical stimulus tank. This density of fish was chosen on the basis that the volume of the chemical stimulus tanks was ~5 times that of the visual stimulus tanks, thus this was an attempt to match the intensity of the visual and chemical stimuli that were to be provided. A third chemical stimulus tank was used to contain a supply of aged water for use as a control. The tanks also contained artificial plants and shelter. The mosquitofish were fed on commercial flaked fish food, and the gudgeon were fed on freshly killed mosquitofish. The fish were not fed within 6 h of the experiments starting. At least 3 h before the experiments began, depending on the treatment, either 8 mosquitofish or 2 gudgeon were added to one of the visual stimulus tanks. These numbers were selected to ensure that the density of fish in the visual stimulus tanks was approximately the same as that in the chemical stimulus tanks. Immediately prior to the beginning of each trial, the valves controlling flow from the chemical stimulus tanks were turned on. One valve provided cues from one of the chemical stimulus tanks, whereas the alternative provided the control water input. A single fish (the focal fish) was haphazardly netted from a different holding tank to that of the stimulus fish and added to a clear perforated plastic cylinder, 9 cm in diameter, that was positioned in the middle of the experimental tank. After 2 min, the cylinder was lifted remotely and the fish was allowed to explore the tank for 5 min. These periods were selected on the basis of prior dye tests: 2 min was sufficient for some chemical cues to reach the center of the tank; 7 min was the limit at which we could still be sure that the chemical cues had not entered the opposite outer zone. Once each trial was completed, the focal fish was removed, measured, and sexed, the valves were turned off, the water was emptied, and the tank was cleaned and replenished with fresh water. To control for side bias, the visual and chemical inputs were switched every other trial. Each focal fish was used only once. Visual stimulus fish were exchanged after every 4 trials.

Each trial was filmed using a Logitech webcam. From this film, we recorded the times taken by the focal fish to enter the outer zone nearest the cue source (hereafter referred to as the target zone) and the total amount of time spent by

the focal fish in the target zone over the 5-min experimental period. The target zone represents the area of the tank where the visual and chemical cues were most concentrated. Furthermore, the use of a clearly delineated zone for our response variables is also designed to reflect an area within which the focal fish could be considered to be shoaling with a conspecific stimulus group or would be at maximum risk of an attack from the predators.

Experiment 1: short-range use of visual cues, chemical cues, and combined multimodal cues by mosquitofish for recognition of conspecifics

Conspecific stimulus was provided at one side of the experimental tank, whereas no stimulus was provided at the other side. We ran 4 treatments: 1) visual cues only, where focal fish were provided with visual cues, coupled with control “blank” water drawn from chemical stimulus tanks that contained no fish; 2) chemical cues only, where focal fish were provided with chemical cues but the visual stimulus tanks contained no fish; 3) aligned multimodal cues: visual and chemical conspecific cues provided in combination; 4) conflicting multimodal cues: visual cues of conspecifics provided in combination with chemical cues of predators.

Experiment 2: the short-range use of visual cues, chemical cues, and combined multimodal cues by mosquitofish for predator recognition

Predator stimulus was provided at one side of the experimental tank, whereas no stimulus was provided at the other side. We ran the treatments on this basis, as described in Experiment 1. In treatment (4), conflicting cues were established by providing visual cues of predators in combination with chemical cues of conspecifics.

Control

To examine how long it took for focal fish to enter a given outer zone and how much time it spent in that outer zone, we ran a control without conspecific or predator stimulus. To allow direct comparison with the experimental treatments, we added a control water input at either end of the tank. Prior to each trial, we randomly selected either the left or the right outer zone as our target zone. Throughout all the experiments, no focal fish was used more than once. Finally, all experiments were conducted “blind” in that the experimenter, a research assistant, was not aware of the hypotheses that were being tested.

Analysis

Q-Q plots and Shapiro–Wilks tests were performed to test for normality of data and Levene’s test was used to test for homogeneity of variances. Comparisons of the time taken to enter the target zone and the time spent in the target zone throughout the experiment across groups were made using analysis of variance (ANOVA) with post hoc Student–Newman–Keuls tests. In addition, we contrasted each treatment against data provided by the control using an independent samples *t*-test. Finally, the analysis described above allowed us to assess the effect of changing chemical cues when visual cues were held constant in the multimodal treatments. In order to examine the effect of changing visual cues when the chemical cues were held constant, we compared across the different experiments. Where multiple *t*-tests were conducted, we adjusted the alpha value using a sequential Bonferroni approach (Rice 1989)

RESULTS

Experiment 1: short-range use of visual cues, chemical cues, and combined visual and chemical cues by mosquitofish for conspecific social recognition

There were significant differences across treatments both in time taken to enter the target zone (ANOVA: $F_{3,60} = 3.13$, $P = 0.032$; see Figure 1a) and total time spent in the target zone (ANOVA: $F_{3,60} = 5.47$, $P = 0.002$; see Figure 1b). Focal fish that had access to aligned multimodal cues entered the target zone sooner than focal fish in all other treatments and faster than the control. Fish that had access to visual, chemical, and aligned multimodal cues spent more time overall in the target zone than either fish with access to conflicting cues or control fish.

Experiment 2: the short-range use of visual cues, chemical cues, and combined visual and chemical cues by mosquitofish for predator recognition

There were significant differences across treatments in time taken to enter the target zone (ANOVA: $F_{3,60} = 3.57$, $P = 0.019$; see Figure 2a) but not in terms of total time spent in the target zone (ANOVA: $F_{3,60} = 2$, $P = 0.12$; see Figure 2b). Focal fish that had access to visual cues only and those with access to aligned visual and chemical cues took longer to enter the target zone than the control, or than focal fish that had access to chemical cues only or to conflicting cues. Fish

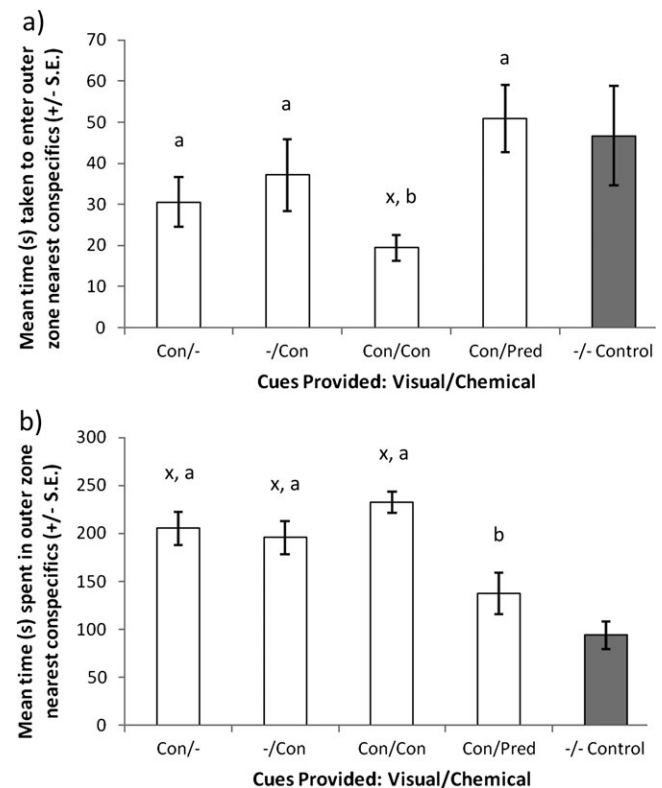


Figure 1
Mean (\pm standard error) time in seconds (a) taken by the focal fish to enter the outer zone nearest the conspecific stimulus and (b) spent by the focal fish in the outer zone nearest the conspecific stimulus compared with a control. Different treatments are shown; con, conspecific and pred, predator. “x” denotes a significant difference from the control. Letters “a” and “b” denote homogeneous subsets as determined by the Student–Newman–Keuls test. Error bars show standard error. $N = 16$ for each treatment.

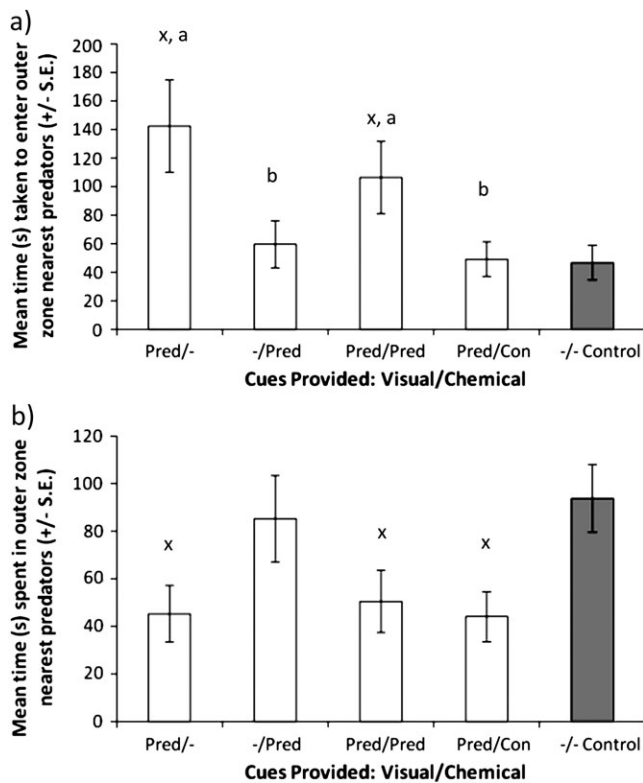


Figure 2

Mean (\pm standard error) time in seconds (a) taken by the focal fish to enter the outer zone nearest the predator stimulus and (b) spent by the focal fish in the outer zone nearest the predator stimulus compared with a control. Different treatments are shown; con, conspecific and pred, predator. "x" denotes a significant difference from the control. Letters "a" and "b" denote homogeneous subsets as determined by the Student–Newman–Keuls test. Error bars show standard error. $N = 16$ for each treatment.

that had access to visual cues only, or to aligned multimodal cues or to conflicting multimodal cues spent less time overall in the target zone than control fish.

Cross-treatment comparisons

Fish approached conspecific visual cues faster than predator visual cues when each was presented in conjunction with predator chemical cues (independent samples t -test: $t_{30} = 2.16$, $P = 0.039$). Fish also approached conspecific visual cues faster than predator visual cues when each was presented in conjunction with conspecific chemical cues (independent samples t -test: $t_{30} = 2.35$, $P = 0.025$).

Fish spent more time in a target zone next to conspecific visual cues than in a target zone next to predator visual cues when each was presented in conjunction with predator chemical cues (independent samples t -test: $t_{30} = 3.45$, $P = 0.002$). Fish also spent more time in a target zone next to conspecific visual cues than in a target zone next to predator visual cues when each was presented in conjunction with conspecific chemical cues (independent samples t -test: $t_{30} = 12.33$, $P < 0.001$).

DISCUSSION

Across all trials, fish with access to conflicting multimodal cues behaved in a generally risk-averse manner in terms of the time spent near either visual or chemical predator cues, demon-

strating attention to multiple sensory cues in their behavioral decisions. The presence of predator chemical cues in proximity to visual cues of a conspecific shoal reduced the time that fish spent in the target zone next to those conspecifics in comparison not only with when conspecific chemical cues were present but also when no chemical cues were present. However, there was no difference between fish with aligned or conflicting cues in their tendency to avoid the predator target zone over the course of the trials and both spent less time in the predator target zone than the control. At first glance, these results are potentially confusing because prey fish typically increase their shoaling tendency when confronted by predator cues (Hoare et al. 2004), so one might expect closer association with conspecific cues when cues relating to risk are present. However, focal fish had to balance any motivation to locate conspecifics with the conflicting imperative to move away from a cue relating to risk; the outcome of this trade-off reveals a risk-averse approach following the detection of predator cues under these circumstances. Many examples of deceit in animal signaling, particularly those used by predators to deceive prey, are often concentrated primarily on one sensory modality. For example, many species of bolas spider (*Mastophora* spp.) produce pheromones that mimic the female sex pheromones of moths in order to lure male moths (Yeargan 1994; Haynes and Yeargan 1999), whereas female fireflies (*Photuris* spp.) use visual cue deception to lure heterospecific male fireflies (*Photinus* spp.) (Eisner et al. 1997). It is likely to be substantially more difficult to enact deceit in more than one sensory modality; hence, it makes clear adaptive sense to respond to multimodal sensory information. In mate choice decisions, the assessment of multimodal cues can often allow the collection of important additional information rather than different sensory cues simply acting as a back up to each other (Candolin 2003). In the same sense that multimodal signaling in animals to an extent enforces honesty (Hebets and Papaj 2005), so avoiding reliance on a single modality can potentially reduce the likelihood of confusion and deceit. Our results suggest that if fish have access to more than one kind of cue, then they are capable of attending to all the available cues and do not always simply discount some types of sensory information in favor of others in a stereotypic hierarchical fashion. This fact is likely to be of key importance in maximizing accuracy in decision making and resolving conflicts in the sensory information that they gather. In the present experiments, the cues were clearly communicated because this was an important part of our study to examine potential trade-offs in the use of different sensory information and how animals resolve informational conflict. If it were the case that either visual or chemical communication were compromised in some way, for example, if light levels were manipulated or if the chemical cues were diluted, then the animals may make a strategic shift to rely more heavily on one or other sensory modality as suggested by a sensory compensation model (Abjornsson et al. 1997; Hartman and Abrahams 2000; see also Chapman et al. 2010).

Nonetheless, the pattern is very different in terms of the latency to approach the different visual stimuli because conflicted fish behaved differently to fish with aligned cues. Conflicted fish were slower to approach conspecific visual cues and faster to approach predator visual cues than fish with access to aligned cues. This might suggest that, even over this short range, chemical cues are used first, then visual cues. However, a comparison across treatments reveals that fish presented with conspecific visual cues and predator chemical cues entered the target zone sooner than fish presented with aligned predator visual and chemical cues. In the same way, fish presented with predator visual cues and conspecific chemical cues entered the target zone less quickly than fish

presented with aligned conspecific visual and chemical cues. Given that the only difference in the treatments in both cases relates to which visual cues are available, it is clear that the fish are indeed attending to all the available sensory information to guide even their initial decisions. Nonetheless, despite the presence of cues relating to risk in each of the conflicting cues treatments, the fish showed no tendency to actively avoid the target zone, in the sense that they entered the target zone as quickly as the controls. Hence, it appears that the presence of conspecific cues in some form attracted the focal fish, even when cues relating to danger were present or at least counteracted the presence of the cues relating to danger. A crucial predictor of success for ambush predators is the distance between themselves and the prey when an attack is launched (Savino and Stein 1989; Price and Mensinger 1999), hence this initial response of the focal fish to approach the source of a conspecific cue regardless of the associated predator cue could be associated with considerable risk. Whether this can be regarded as a case in which the fish was simply confused and therefore simply behaving suboptimally (thereby opening the possibility of deception by a predator), whether the fish was approaching in an attempt to gain further information (Pitcher et al. 1986), or whether the imperative for a social species to seek conspecifics sometimes overrides all else (Ward et al. 2008) is difficult to determine.

Across all experiments, fish with access to aligned multimodal cues were able to make relatively accurate decisions, outperforming the control in each case. A similar pattern of combined aligned cues provoking a stronger response than isolated cues has been reported several times before both in terms of the detection of predators and the detection of conspecifics. In the context of cue use under a predation threat, additivity has been shown in marine gobies (*Asterropteryx semipunctatus*) (McCormick and Manassa 2008), in freshwater perch (*Perca fluviatilis*) (Mikheev et al. 2006), and in hermit crabs (*Pagurus bernhardus*) (Dalesman and Inchley 2008), whereas in a social context, additivity has been shown in swordtails (*Xiphophorus helleri*) (Coleman and Rosenthal 2006) and in sticklebacks (Ward et al. 2002). In the present study, the latency to move to the conspecific target zone when using isolated chemical or isolated visual cues was not different to the control, suggesting that the initial location of shoal mates is augmented by the presence of multiple cues. Despite this, across all trials, fish with access to visual-only information performed almost as well as fish with multimodal cues, indicating the primary value of visual information over such short ranges. By contrast, fish with access to chemical-only information appeared to perform relatively poorly, particularly in the predator experiment, where they made seemingly risky decisions in comparison with other cues treatments. This is despite the fact that the predators had been fed on a diet of mosquitofish and were likely contributing cues derived from digestion, which should provoke the strongest aversive response in the prey (Schoeppner and Relyea 2009). One possible explanation is that, having detected through chemical means the existence of a threat in the locality, the fish were trying to update their information in order to be better able to respond appropriately to the level of danger. Although failing to flee a threat may incur obvious risks, if prey animals respond indiscriminately to signs of danger by adopting anti-predator behavior, then they may incur considerable opportunity costs, losing chance to feed or mate, hence prey animals should respond according to the perceived levels of risk (Kats and Dill 1998; Foam, Harvey, et al. 2005; Foam, Mirza, et al. 2005; Ferrari et al. 2008, 2009). In order to be better able to make informed decisions, prey animals require accurate information. Many species gather information by inspecting potential predators (Pitcher et al. 1986; Brown and

Godin 1999; Brown et al. 2000; Brown and Dreier 2002). In such cases, the predator may often be detected first on the basis of chemical cues, although approaching the predator may yield additional chemical information, plus visual information relating to its locality and behavior (Licht 1989; Murphy and Pitcher 1997; Brown and Magnavacca 2003). Many prey species manifest a graded threat-sensitive response based on visual information, but a more generalized response to predator chemical cues, hence visual cues may be needed to accurately determine the level of risk posed by a given predator (Chivers et al. 2001; Smith and Belk 2001). This pattern of a generalized response to chemical predator cues is also found in other taxa, such as reptiles (Webb et al. 2009) and may be indicative of differences in the information content of visual and chemical information (although see Ferrari et al. 2006).

Our experiments suggest a difference between the initial response and the response over a longer period of potential prey animals to conflicting sensory information. It would be useful to try and resolve whether this is due to error by focal fish or due to their response to seek more information. Furthermore, it would be valuable to further examine conflicts in sensory information by manipulating aspects of the visual and chemical information provided, perhaps by combining predator and prey stimulus cues simultaneously into a single modality or by attempting to alter the prey's perception of the threat posed by the predator by feeding it a different diet beforehand.

The authors would like to thank Mike Webster, Ben Hatchwell, Eileen Hebets, and Ben Chapman for helpful comments and suggestions that greatly improved this manuscript.

REFERENCES

- Abjornsson K, Wagner BMA, Axelsson A, Bjerselius R, Olsen KH. 1997. Responses of *Acilius sulcatus* (Coleoptera: Dytiscidae) to chemical cues from perch (*Perca fluviatilis*). *Oecologia*. 111: 166–171.
- Aeschlimann PB, Haberli MA, Reusch TBH, Boehm T, Milinski M. 2003. Female sticklebacks *Gasterosteus aculeatus* use self-reference to optimize MHC allele number during mate selection. *Behav Ecol Sociobiol*. 54:119–126.
- Aksnes DL, Utne ACW. 1997. A revised model of visual range in fish. *Sarsia*. 82:137–147.
- Barata EN, Hubbard PC, Almeida OG, Miranda A, Canario AV. 2007. Male urine signals social rank in the Mozambique tilapia (*Oreochromis mossambicus*). *BMC Biol*. 5:54.
- Barbero F, Thomas JA, Bonelli S, Balletto E, Schonrogge K. 2009. Queen ants make distinctive sounds that are mimicked by a butterfly social parasite. *Science*. 323:782–785.
- Brown GE. 2003. Learning about danger: chemical alarm cues and local risk assessment in prey fishes. *Fish Fish*. 4:227–234.
- Brown GE, Dreier VM. 2002. Predator inspection behaviour and attack cone avoidance in a characin fish: the effects of predator diet and prey experience. *Anim Behav*. 63:1175–1181.
- Brown GE, Godin JGJ. 1999. Who dares, learns: chemical inspection behaviour and acquired predator recognition in a characin fish. *Anim Behav*. 57:475–481.
- Brown GE, Magnavacca G. 2003. Predator inspection behaviour in a characin fish: an interaction between chemical and visual information? *Ethology*. 109:739–750.
- Brown GE, Paige JA, Godin JGJ. 2000. Chemically mediated predator inspection behaviour in the absence of predator visual cues by a characin fish. *Anim Behav*. 60:315–321.
- Candolin U. 2003. The use of multiple cues in mate choice. *Biol Rev*. 78:575–595.
- Chapman BB, Morrell LJ, Tosh CR, Krause J. 2010. Behavioural consequences of sensory plasticity in guppies. *Proc R Soc Lond B Biol Sci*. 277:1395–1401.
- Chivers DP, Mirza RS, Bryer PJ, Kiesecker JM. 2001. Threat-sensitive predator avoidance by slimy sculpins: understanding the

- importance of visual versus chemical information. *Can. J Zool.* 79: 867–873.
- Coleman SW, Rosenthal GG. 2006. Swordtail fry attend to chemical and visual cues in detecting predators and conspecifics. *PLoS One*. 1:4.
- Dalesman S, Inchley CJ. 2008. Interaction between olfactory and visual cues affects flight initiation and distance by the hermit crab, *Pagurus bernhardus*. *Behaviour*. 145:1479–1492.
- Eisner T, Goetz MA, Hill DE, Smedley SR, Meinwald J. 1997. Firefly 'femmes fatales' acquire defensive steroids (lucibufagins) from their firefly prey. *Proc Natl Acad Sci U S A*. 94:9723–9728.
- Ferrari MCO, Messier F, Chivers DP. 2006. The nose knows: minnows determine predator proximity and density through detection of predator odours. *Anim Behav*. 72:927–932.
- Ferrari MCO, Messier F, Chivers DP. 2008. Larval amphibians learn to match antipredator response intensity to temporal patterns of risk. *Behav Ecol*. 19:980–983.
- Ferrari MCO, Sih A, Chivers DP. 2009. The paradox of risk allocation: a review and prospectus. *Anim Behav*. 78:579–585.
- Foam PE, Harvey MC, Mirza RS, Brown GE. 2005. Heads up: juvenile convict cichlids switch to threat-sensitive foraging tactics based on chemosensory information. *Anim Behav*. 70:601–607.
- Foam PE, Mirza RS, Chivers DP, Brown GE. 2005. Juvenile convict cichlids (*Archocentrus nigrofasciatus*) allocate foraging and antipredator behaviour in response to temporal variation in predation risk. *Behaviour*. 142:129–144.
- Giske J, Huse G, Fiksen O. 1998. Modelling spatial dynamics of fish. *Rev Fish Biol Fish*. 8:57–91.
- Hartman EJ, Abrahams MV. 2000. Sensory compensation and the detection of predators: the interaction between chemical and visual information. *Proc R Soc Lond B Biol Sci*. 267:571–575.
- Hasler AD, Cooper JC. 1976. Chemical cues for homing salmon. *Experientia*. 32:1091–1093.
- Haynes KF, Yeargan KV. 1999. Exploitation of intraspecific communication systems: illicit signalers and receivers. *Ann Entomol Soc Am*. 92:960–970.
- Hebets EA, Papaj DR. 2005. Complex signal function: developing a framework of testable hypotheses. *Behav Ecol Sociobiol*. 57: 197–214.
- Herbert-Read JE, Logendran D, Ward AJW. 2010. Sensory ecology in a changing world: salinity alters conspecific recognition in an amphidromous fish, *Pseudomugil signifer*. *Behav Ecol Sociobiol*. 64: 1107–1115.
- Hoare DJ, Couzin ID, Godin JGJ, Krause J. 2004. Context-dependent group size choice in fish. *Anim Behav*. 67:155–164.
- Johnstone RA. 1996. Multiple displays in animal communication: 'Backup signals' and 'multiple messages'. *Philos Trans R Soc Lond B Biol Sci*. 351:329–338.
- Kats LB, Dill LM. 1998. The scent of death: chemosensory assessment of predation risk by prey animals. *Ecoscience*. 5:361–394.
- Licht T. 1989. Discriminating between hungry and satiated predators—the response of guppies (*Poecilia reticulata*) from high and low predation sites. *Ethology*. 82:238–243.
- McCormick MI, Manassa R. 2008. Predation risk assessment by olfactory and visual cues in a coral reef fish. *Coral Reefs*. 27: 105–113.
- Mikheev VN, Wanzenböck J, Pasternak AF. 2006. Effects of predator-induced visual and olfactory cues on 0+perch (*Perca fluviatilis* L.) foraging behaviour. *Ecol Freshw Fish*. 15:111–117.
- Murphy KE, Pitcher TJ. 1997. Predator attack motivation influences the inspection behaviour of European minnows. *J Fish Biol*. 50: 407–417.
- Pitcher TJ. 1980. Some ecological consequences of fish school volumes. *Freshw Biol*. 10:539–544.
- Pitcher TJ, Green DA, Magurran AE. 1986. Dicing with death—predator inspection behavior in minnow shoals. *J Fish Biol*. 28: 439–448.
- Price NN, Mensinger AF. 1999. Predator–prey interactions of juvenile toadfish, *Opsanus tau*. *Biol Bull*. 197:246–247.
- Rice WR. 1989. Analyzing tables of statistical tests. *Evolution*. 43: 223–225.
- Savino JF, Stein RA. 1989. Behavior of fish predators and their prey—habitat choice between open water and dense vegetation. *Environ Biol Fish*. 24:287–293.
- Schoeppner NM, Relyea RA. 2009. Interpreting the smells of predation: how alarm cues and kairomones induce different prey defences. *Funct Ecol*. 23:1114–1121.
- Seghers BH. 1974. Schooling behavior in guppy (*Poecilia reticulata*)—evolutionary response to predation. *Evolution*. 28:486–489.
- Smith ME, Belk MC. 2001. Risk assessment in western mosquitofish (*Gambusia affinis*): do multiple cues have additive effects? *Behav Ecol Sociobiol*. 51:101–107.
- Uetz GW, Roberts JA. 2002. Multisensory cues and multimodal communication in spiders: insights from video/audio playback studies. *Brain Behav Evol*. 59:222–230.
- Utne-Palm AC. 2002. Visual feeding of fish in a turbid environment: physical and behavioural aspects. *Mar Freshw Behav Physiol*. 35:111–128.
- Ward AJW, Axford S, Krause J. 2002. Mixed-species shoaling in fish: the sensory mechanisms and costs of shoal choice. *Behav Ecol Sociobiol*. 52:182–187.
- Ward AJW, Sumpter DJT, Couzin LD, Hart PJB, Krause J. 2008. Quorum decision-making facilitates information transfer in fish shoals. *Proc Natl Acad Sci U S A*. 105:6948–6953.
- Ward AJW, Webster MM, Hart PJB. 2007. Social recognition in wild fish populations. *Proc R Soc Lond B Biol Sci*. 274:1071–1077.
- Webb JK, Du WG, Pike DA, Shine R. 2009. Chemical cues from both dangerous and nondangerous snakes elicit antipredator behaviours from a nocturnal lizard. *Anim Behav*. 77: 1471–1478.
- Webster MM, Atton N, Ward AJW, Hart PJB. 2007. Turbidity and foraging rate in threespine sticklebacks: the importance of visual and chemical prey cues. *Behaviour*. 144: 1347–1360.
- Webster MM, Goldsmith J, Ward AJW, Hart PJB. 2007. Habitat-specific chemical cues influence association preferences and shoal cohesion in fish. *Behav Ecol Sociobiol*. 62:273–280.
- Wiley RH. 1983. The evolution of communication: information and manipulation. In: Halliday TR, Slater PJB, editors. *Animal Behaviour*. Vol. 2, Communication. Oxford: Blackwell Scientific Publications. p. 156–189.
- Wisenden BD. 2000. Olfactory assessment of predation risk in the aquatic environment. *Philos Trans R Soc Lond B*. 355: 1205–1208.
- Wyatt TD. 2003. Pheromones and animal behaviour: communication by smell and taste. Cambridge: Cambridge University Press.
- Yeargan KV. 1994. Biology of bolas spiders. *Ann Rev Entomol*. 39: 81–99.