Preface

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Most animal behaviors rely on the integration of information from a number of both external and internal sensory sources. The assembly of this information, arriving via different nervous system pathways, into a coherent and useful ‘gestalt’ upon which appropriate behavioral responses can be generated is a fundamental role of the brain and a major focus of cognitive neuroscience [e.g., Stein and Meredith, 1993]. Although a number of neurophysiological studies have identified central sites of multimodal sensory integration (e.g., the superior colliculus) for simple behaviors (e.g., orienting responses) [Sparks and Groh, 1988], relatively few studies have examined the exact roles played by different sensory systems (or submodalities within a system) in controlling complex behaviors such as predation and courtship. Does the relative contribution of a given modality change during the course of the behavior, for example between the time of initial prey detection and the final prey capture event? Is there evidence for range fractionation? What is the multisensory contribution to decision making processes, such as determining what direction to turn or when to initiate the final strike during prey capture behavior? Are different aspects or features of the stimulus source encoded by different sensory systems and if so, how is this information parsed or combined in both spatial and temporal domains? Do sensory hierarchies play a role and if so, what factors determine the hierarchy?

To address some of these questions, we organized a symposium on the Multisensory Guidance of Complex Behaviors at the 6th International Congress of Neuroethology in Bonn, Germany. In choosing symposium participants and contributors to this special issue of *Brain, Behavior and Evolution*, we quite naturally gravitated towards researchers working on fishes. As well as being near and dear to our own research ‘hearts’, fish have several ‘extra’ senses (e.g., electrosense and lateral line) in addition to the more familiar vision, hearing, touch, taste and smell of most terrestrial animals and thus they provide a rich array of sensory systems for investigating multisensory questions. Furthermore, the existence of several close – (e.g., electrosense and lateral line) and long – (e.g., vision and audition) range systems provides a useful construct for examining questions of range fractionation.

In the first paper of this issue, Braun and colleagues tackle the difficult and long-standing question of how or if auditory and lateral line systems contribute to directional behaviors involving the ability of fish to localize moving or vibratory sources such as predators or prey. They use computational modeling to reveal potential contributions from submodalities in both systems and evaluate these models and current behavioral data in light of four postulated ways (fractionation, complementation, accessory stimulation and synergy) in which multiple senses can interact.

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New follows with a series of behavioral studies on the prey capture behavior of two diurnal predators, the muskellunge and the largemouth bass. Videotapes of free-field feeding behaviors of these fishes with and without suppression of vision and/or the lateral line are quantitatively analyzed to examine the relative roles played by each sensory system in the sequential organization of three distinct phases of the behavior.

Prey capture behavior continues as an important focus of multisensory investigations as Montgomery and colleagues summarize their studies on the integration of hydrodynamic, chemosensory, tactile and visual information to different types of prey capture strategies in different species, including odor-gated rheotaxis by banded kokopu and hydrodynamic trail following by trout. Likewise, Nelson and colleagues examine the contribution of the lateral line and both active and passive electrosense to the prey capture behavior of weakly electric, black ghost knifefish. They combine computational models of electrosensory and mechanosensory stimuli with actual prey strike trajectories from infrared video recordings to reconstruct spatial images of the prey along the sensory surface of the fish during the prey capture behavior.

Rojas and Moller exploit the natural tendency of another weakly electric fish, the elephant nose fish, to seek shelter during the day. With a series of behavioral experiments employing cue-elimination and cue-conflict designs, they examine the relative roles played by vision and electrosense submodalities in the ability of these fish to establish and maintain spatial relationships to shelters with different electrical and optical properties.

Last, but not least, Uetz and Roberts take us out of the water to examine the effects of visual and vibratory cues on the receptivity of female wolf spiders to males during courtship. They apply several experimental techniques, including video/audio playback of digitized signals and cue-isolation and cue-conflict designs to tease apart elements of multimodal signaling and its effectiveness in attracting females. By studying the effectiveness of these cues in closely related species, they also examine the evolution of multisensory strategies, asking the fundamental question: if single modes of courtship communication are sufficient for some species, why have others evolved multiple modes?

At least six overriding principles have emerged from the papers in this issue: (1) Different submodalities of the same sensory system can underlie different behavioral tasks. For example, the ability of fish to orient to ambient currents in a stream (rheotaxis) is mediated by one class of lateral line receptors (superficial neuromasts), whereas

their ability to orient to moving sources (e.g., prey) is mediated by a separate class (canal neuromasts) [Montgomery et al., 2002; Braun et al., 2002]. (2) Different sensory systems (or submodalities within a given system) can extract fundamentally different types of information to accomplish a single behavioral objective. The ability of many terrestrial insects (e.g., moths), aquatic invertebrates (e.g., crabs and lobsters) and fishes to track odor plumes and to locate odor sources, for example, involves a chemo-based detection and orientation to the odor source in combination with a mechanosensory-based rheotaxis to the currents that distribute the odor trail [Montgomery et al., 2002]. As a second example, pressure-sensitive components of the fish inner ear can extract information on the polarity (e.g., advancing or receding) of a moving source (e.g., a predator), whereas acceleration-sensitive components extract directional information (e.g., advancing from the left or right) [Braun et al., 2002]. (3) The relative contribution of different sensory systems to any given behavior can change over time or as a function of distance to the stimulus source. The prey capture behavior of muskellunge and bass, for example, consists of an initial orienting response and subsequent long-range stalking phase that are guided entirely by visual cues and a final, short-range strike phase guided by both visual and lateral line cues [New, 2002]. Likewise, some species of spiders produce visual and vibratory signals separately at different times during pre-copulatory behavior [Uetz and Roberts, 2002]. (4) There are species-specific differences in the relative contributions of different sensory systems to a given behavior. The prey capture behavior of muskellunge and bass [New, 2002], and that of both the black ghost knifefish [Nelson et al., 2002] and the Lake Michigan mottled sculpin [Braun et al., 2002] can be roughly divided into three phases: an initial orienting, approach and final strike phase. However, the initial orienting response of diurnally active muskie or bass is mediated by a long-range modality (vision), whereas that of nocturnal species (mottled sculpin) or species living in turbid environments (black ghost knifefish) is mediated by short-range modalities (lateral line or electrosense). Similarly, wolf spiders within a single taxonomic clade exhibit species-specific differences in their reliance on visual and vibratory communication during courtship [Uetz and Roberts, 2002]. (5) The relative contributions of different sensory systems might depend on dynamically changing environmental factors. As an example, the electrosense may dominate the prey capture behavior of weakly electric, nocturnal fish at low water conductivities, but not at higher water conductivities where the mechanosensory

lateral line may play a larger role [Nelson et al., 2002]. Similarly, multisensory contributions to shelter-seeking behavior by weakly electric fish vary with available visual cues and shelter characteristics [Rojas and Moller, 2002]. (6) Simultaneous use of different sensory modalities can enhance decision-making processes or overall behavioral performance in synergistic ways. In some species of wolf spiders, for example, females are most receptive to courtship displays by males when both visual and vibratory cues of the display are present [Uetz and Roberts, 2002]. Likewise, Rojas and Moller show that vision and two electrosense submodalities interact in synergistic ways to improve the ability of elephant nose fish to maintain proximity to their shelters.

From the examples given above and others in this issue, it can be seen that multimodal sensory interactions in the guidance of complex behaviors are extremely labile. For any given behavior (e.g., prey capture behavior), both the type and degree of interaction can vary as a function of life style (e.g., nocturnal vs. diurnal), habitat (e.g., ben-

thic vs. pelagic), stimulus source (e.g., epibenthic vs. benthic prey) and prevailing environmental conditions (e.g., low water conductivity or ambient light level vs. high water conductivity or ambient light level). Thus, a thorough understanding of multisensory processing will require not only an ethologically valid context, but an ecologically and evolutionary valid one as well.

The computational and experimental approaches described in this issue focus on the relative contributions of different sensory modalities to natural behaviors, rather than on specific ways in which the central nervous system integrates information from the various modalities to effect behavior. Behavior is, of course, the inevitable end product of multisensory integration (and sensory/motor integration) in the CNS. Thus, we hope that future studies on central mechanisms of multisensory integration will include natural behaviors of different species in ecologically-valid contexts and that they will furthermore test, accept, reject, modify or extend many of the ideas put forth in this issue.

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