

NEUROBIOLOGY

Cross-modal sensory transfer: Bees do it

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Animal sensory systems acquire information about the physical world by transforming external stimuli into signals that can be read and interpreted by the nervous system. Animals possess several senses that provide separate streams of information based on different physical stimuli. However, objects and environments contain inherently multimodal information, and so neurobiologists have sought to define the mechanisms by which information is processed when received via different senses (1). Cross-modal recognition—the ability to transfer information across senses, irrespective of the sense that first accessed that information—was thought to be a highly complex cognitive capacity, constrained to vertebrates. Now, on page xxx of this issue, Perry *et al.* (3) show that bumblebees are capable of performing the same task.

Humans execute spontaneous cross-modal recognition fairly easily (2); for example, people often rummage blindly through pockets or handbags to find, by touch, a set of keys that they first encountered visually. Cross-modal recognition is a useful skill, not only for fishing out our keys, but crucially, for increasing the flexibility of our object-recognition systems. The remarkable finding by Perry *et al.* illustrates that tiny invertebrates, with brain structures that differ greatly from those of vertebrates, also can experience an object with one sensory modality and later, recognize that same object with a different sensory modality.

Simple forms of cross-modal information transfer, which are based on direct associations between two specific stimuli, have been observed in various animal groups, including insects (4, 5). However, cross-modal object recognition requires additional and more complex conditions—in particular, that the two senses provide information that is matched in content. This means that both senses have to provide information about the same characteristic of an object, for example, its shape or surface structure. In addition, the sensory inputs must be encoded in a way that allows temporally disjointed information from two senses to be identified as identical, despite the fact that these senses rely on different physical stimuli. Thus, characteristic object features are stored in a neuronal representa-

tion that can be accessed by multiple senses. Up to now, spontaneous cross-modal object recognition has only been described in mammalian species (humans, apes, monkeys, dolphins, and rats) (6–8) and in one aquatic creature—the weakly electric elephantnose fish (9).

In an elegant experiment, Perry *et al.* trained bumblebees to discriminate two differently shaped objects (cubes and spheres) using only touch (in darkness) or only vision (in light, but barred from touching the objects). After training, the bumblebees discriminated between the same objects using only the other sensory information. This shows that, the brain encoded the sensory input in a way that allowed the two sensory channels to exchange information and compare and match object-related inputs.

The mechanisms by which bees achieve this task have yet to be elucidated. Perhaps the bee's brain stores a representation of the object in a way that allows it to be accessed and understood across different sensory systems. The sensory information would need to be integrated to form a representation that is independent of the sensory modality through which the information was introduced (that is, both senses use a matched encoding format). This would enable bees to recognize objects cross-modally without any previous experience, and cross-modal object recognition would not require training. Alternatively, information that originates from multiple senses might initially be unmatched in format, and cross-modal object recognition could depend on sensory experience and learning. In this case, bees might have learned to associate visual and tactile inputs of basic features common in other environmental objects when exposed to these features in the past. For example, a bee might have learned to associate a visual and a tactile image of a curved edge or a corner. Subsequently, these associations would generalize to new objects and new situations.

Whatever the mechanism, cross-modal object recognition requires storage, in the brain, of a representation of the object's features that can be accessed by different senses. This would imply that an object can be recognized with a sense through which it had never been experienced, before. Perry *et al.* show that this cognitive capability can be achieved by the brain of an insect, which contains just a

small fraction of the number of neurons in a vertebrate brain (10).

How the organization of sensory systems achieves cross-modal object recognition is a key unanswered question. Sense organs respond to the physical stimuli of the outside world and transduce them into a series of action potentials encoding the specific stimulus parameters. Connections are then made with nerve cells in dedicated sensory nuclei within the brain, which in turn project to subsequent sensory nuclei for further processing (see the figure). To add to the complexity, these following centers also project back to lower processing centers, forming reciprocal circuits. For multisensory integration and cross-modal transfer, information from the different sensory modalities that encode characteristics of the same object must come together, eventually forming a multi-sensory representation of the object. In most cases, scientists still do not know exactly where in the sensory pathway this occurs, particularly in bees and fish, which do not possess specialized cortical structures. One possibility is that higher brain structures, such as the cortex in mammals or the mushroom bodies and central complex in bees, form the anatomical substrate for multisensory representations (6, 11). Alternatively, because crosstalk between the senses also occurs at lower levels (e.g., in the midbrain and diencephalon) (1, 12, 13) and sensory nuclei on different levels are connected in a reciprocal manner, a distributed representation of object properties might occur in several interconnected multi-sensory nuclei (see the figure).

The fact that bees can achieve cross-modal object recognition might have implications for how we think about cognition in general. In humans, scientists assume that this ability involves mental imagery (14) based on internal representations in higher brain centers. Thus it has been argued that this task relies on awareness. Whether that is also the case in bumblebees is a matter of debate as simpler explanations are possible. Whatever the underlying mechanism, the newly found ability of bumblebees to perform cross-modal recognition shows that, like humans, they possess a sensory integration system that allows them to form a complex representation of their world.

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Figure 1: Schematic sketch for cross-modal object recognition representing general principles across animal groups.

In both vertebrates and invertebrates, sense organs (such as eyes for vision or fingertips - antenna in bumblebees - for touch) respond to physical stimuli in the outside world and transfer this information to specific sensory nuclei of the brain, which in turn are connected in a reciprocal manner with secondary nuclei. While sensory pathways start monomodally, in many cases multimodal neurons are found fairly early in the sensory pathway. In higher centers, multimodal sensory nuclei are the norm. In principle, cross-modal sensory transfer might occur at any stage past the first, monomodal sensory nuclei.

