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NEWS & VIEWS

BEHAVIOURAL NEUROSCIENCE

Neurons of imitation

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In songbirds, a class of neurons shows a striking similarity in activity when the bird sings or when it hears a similar song. This mirroring neuronal activity could contribute to imitation.

Songbirds are champion mimics. A nightingale, for example, can imitate at least 60 different songs after a few exposures to each[1]. A young bird learns its species' song through imitation, and the ability is also socially important: a bird on its territory will often respond to an intruder's song by singing a similar song, thus acknowledging the intrusion[2]. What neurons might mediate these imitative and communicative powers? On page 305 of this issue, Prather *et al.*[3] identify a class of brain neurons that are active both when the bird hears a song and when it replies by singing a similar song.

As such, these neurons are reminiscent of the mirror neurons discovered in the monkey brain. These respond similarly whether an action is perceived or performed, and they aroused enormous interest as a possible key to understanding such disparate phenomena as imitation and empathy. Mirror neurons are activated both when a monkey performs a discrete action — such as grasping a small object between thumb and forefinger — and when it sees another monkey or a human do the same[4], but not when the same action is performed without accomplishing the goal (pretending to grasp the object).

To mirror neurons, actions performed or observed are equivalent, so they could mediate imitation — a most mysterious form of learning. How does one know what pattern of muscle contraction corresponds to a particular visual effect? The psychologist William James speculated that infants correlate their random limb movements with the sight of their limbs, thereby forming an association between motor outputs and visual inputs that allows them to infer how others make similar limb movements. But one does not need to spend hours in front of a mirror to imitate the facial expressions of others[5]; nor do French or Italian children need to observe themselves to acquire the facial gestures characteristic of their elders. Mirror neurons may be the link between the sensory information perceived and gestures produced.

Mirror neurons might also facilitate our perception and memory of complex sensory stimuli[6]. For example, a sequence of familiar dance steps could be more easily encoded in memory in terms of the commands that the brain sends to move the limbs than it could by remembering all the small visual changes these limb movements produce. This function of mirror neurons would not be independent of their ability to facilitate imitation. Indeed, it is a common experience, when watching a car chase in a film, to feel oneself involuntarily making small steering or braking movements.

The responses of mirror neurons have led psychologists to propose that they provide a way of inferring the workings of another's mind, and so are essential for the development of social communication and empathy[7]. This has put the emphasis on mirror neurons' higher-level functions. The mirroring neurons Prather and colleagues found in songbirds may also have such functions, but they seem to have more prosaic roles in acquiring motor skills and in learning.

All the likely functions of the songbird mirroring neurons are related to singing. The neurons are located in the brain's principal song-generating nucleus, the high vocal centre

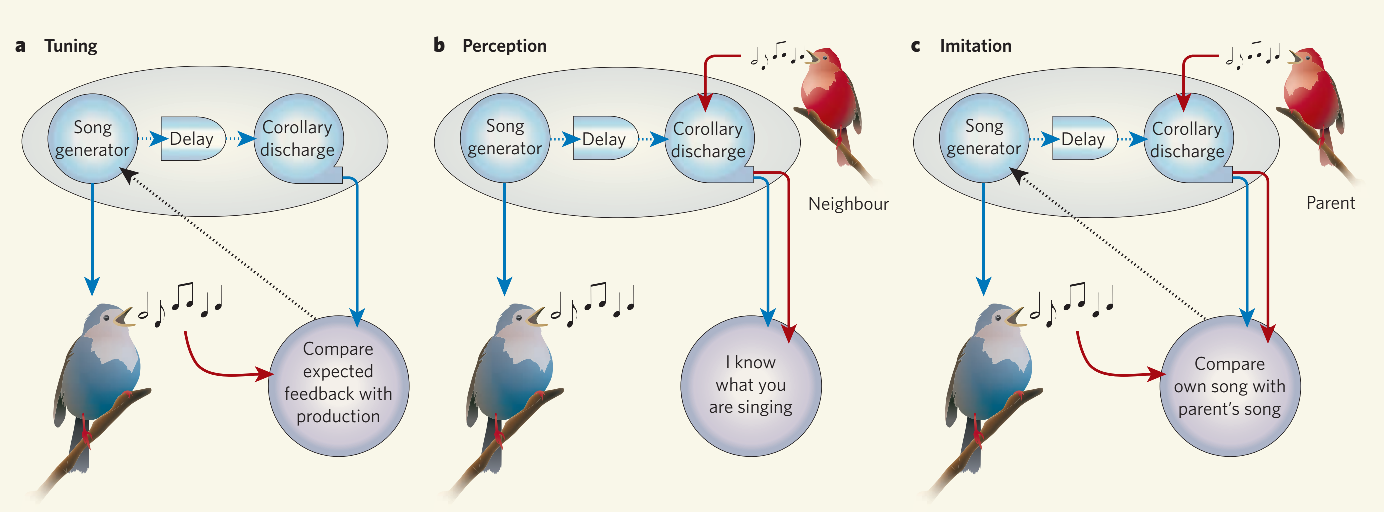

Figure 1 | A singing–listening neuronal connection. The neurons identified by Prather and colleagues[3] could be involved in three sensory-motor processes. **a**, The delayed corollary discharge of song patterns can be simultaneously compared with auditory feedback of the bird's own song, allowing tuning. **b**, The auditory responses (in the mirroring neurons) to songs of a neighbour might be compared with the memory of the corollary discharge produced during singing. This might allow the bird to identify an imitation by that neighbour. **c**, Corollary discharges while singing might be compared with a memory of the mirroring neurons' response to the parent's song. The error may then feed back to the song generator and guide vocal learning during song development, in addition to guidance from auditory input during singing (lowest arrow).

(HVC). Like other neurons in the HVC, they respond to specific songs with highly stereotyped timing of nerve impulses. Curiously, when the bird is singing, these mirroring neurons are deaf to auditory input, meaning that their responses switch between being auditory and being a reflection of motor activity.

Because the HVC is a pre-motor structure, it would be expected that nerve impulses would occur here earlier than the resulting sounds, whereas the auditory responses of the neurons would occur later. But Prather *et al.*[3] find that the timing of nerve impulses from the mirroring neurons of the HVC is the same whether the bird is singing or listening. This remarkable delaying of the motor signal implies that the mirroring neurons are providing a 'corollary discharge' signal, that is, a neural representation of the motor output (the song being sung) encoded in a way that can be readily compared with the auditory input (hearing the song). Thus, these neurons present two solutions to the brain"s main problems in comparing motor outflow with sensory inflow: they form an equivalence between the motor output and the resultng sensory feedback, and they compensate for the delay between them[8].

What functions might this corollary discharge have? Prather and colleagues found a clue by investigating where the projections (axons) of the mirroring neurons go. The HVC has two outputs: one down the motor song pathway to the vocal organ, and the other to the anterior forebrain pathway (AFP), which is required for song learning but not for singing. All of the mirroring neurons project to the AFP, which, in turn, trains the motor song system during song learning by introducing variability into the song patterns[9].

Sending corollary discharge into the AFP might have several functions. First, synchronous responses to hearing and singing might allow tuning of the song (Fig. 1a). While singing, the corollary discharge from the song generator might be compared with the auditory feedback from the resulting song. Such an online comparison might allow adjustments of the song produced[10]. Second, when a bird hears a neighbour imitating its song, its mirroring neurons might send a pattern to the AFP similar to that of the corollary discharge (Fig. 1b). The AFP might then recognize the song, thereby providing an efficient mechanism for the bird to identify its neighbour.

Third, mirroring neurons could be necessary for the gradual process of the bird learning to imitate the songs of its parent (Fig. 1c). The young bird might compare the corollary discharge of its singing with the memory of the responses of the mirroring neurons to the parent's songs, thereby simplifying the comparison and facilitating a gradual improvement in the imitation. Possibly related to this function is that, during the several weeks that song learning takes, many HVC neurons are replaced by others[11]. The mirroring neurons identified by Prather *et al.* belong to a population that is not replaced, but is stable across song development. It is tempting to imagine that this stability keeps the corollary-discharge signal reliable while the song produced is changing, thereby defining a role for these neurons at the centre of the sensory-motor convergence that facilitates vocal imitation[8].

The exciting findings of Prather *et al.*[3] offer the possibility of following the emergence of sensory-motor mirroring as the song becomes increasingly structured and similar to the song being learned. More generally, the mystery of how a neuron can have similar responses to performing and experiencing an action might be clarified by studying which response develops first and how the two responses converge, resulting in a common neural representation. ■

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