Corrections and Retraction

CORRECTIONS

NEUROSCIENCE


The authors note that the legend for Fig. 5 appeared incorrectly. The figure and its corrected legend appear below.

Fig. 5. Role of the dorsal MLR in respiratory modulation during locomotion. (A) Schematic representation of the semi-intact preparation. (B) Respiratory increases following PT stimulation that induced locomotor movements. (C) Close-up of the respiratory bursts during locomotion (Upper) and drawings of tail movements induced by the PT stimulation (Lower). (D) Respiratory increase following PT stimulation after blockade of the dorsal part of the MLR (dMLR) with microinjections of CNQX (1 mM) and APS (500 μM). (E) Close-up of the respiratory bursts during locomotion (Upper) and drawings of tail movements induced by the PT stimulation (Lower). (F) Analysis of all PT stimulation in all lampreys (n = 5 preparations) in control situation (red, n = 15) and after blockade of the dorsal part of the MLR (blue, n = 6). Data were triggered around the beginning of locomotion (i.e., time 0) and were pooled in classes of 15 s. The shaded area around the curves corresponds to the SE of the mean. (G) Similar analysis for locomotor frequency. Dots indicate respiratory bursts. PT, posterior tuberculum; X, vagal motor nucleus.

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The author notes: “Although I included a citation to and a figure from Guenet et al. in my article, the importance of this reference in developing the argument of linkage between terrestrial and aquatic carbon was not properly detailed. Guenet et al. was the first to note the potential interactions between terrestrial and aquatic carbon and the importance of priming effect (PE) in aquatic ecosystems. Additionally, the work for Guenet et al. should be cited in the following sections of the article:

‘On page 19477, left column, second full paragraph, lines 27–30, ‘All the aforementioned scenarios represent the simplified pathways established for priming in soil types’ should instead appear as ‘All the aforementioned scenarios represent the simplified pathways established for priming in soils and natural waters’ (86).’

‘Also on page 19477, middle column, the legend for Fig. 3 should instead appear as ‘Three different priming effects involving LOM and ROM, respectively. These proposed priming effects are soils and natural waters derived from work in soils. Modified from Guenet et al. (86).’

‘Lastly, on page 19477, middle column, first full paragraph, lines 10–14, ‘The mineralization of charcoal, a very recalcitrant form of OC, was shown to increase between 36% and 189% (vs. control) when primed with glucose’ should instead appear as ‘The mineralization of charcoal, a very recalcitrant form of OC, was shown to increase between 36% and 600% (vs. control) when primed with glucose’.”


The authors note that on page 8296, right column, Equations 10 and 11 appeared incorrectly.

The corrected equations appear below.

\[
y_{ij} = \mu + \beta_i + \beta_B(t_i + d_i) + \beta_W(t_i - d_i) + e_{ij} \quad [10]
\]

\[
y_{ij} = \mu + \beta_i + \beta_B t_i + \beta_W t_i + d_i(\beta_B - \beta_W) + e_{ij} \quad [11]
\]
Specific neural substrate linking respiration to locomotion

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AUTHOR SUMMARY

In most animals, including humans, respiration increases during movement and exercise to compensate for an increased energy demand. A number of complementary mechanisms may contribute to informing regions in the brain that control respiration about ongoing motor activities (e.g., muscle contractions). Researchers have identified some of these mechanisms. For instance, chemoreceptors (i.e., cells that detect specific molecules) were found in the brainstem and the carotid body, which is a small body of cells near the carotid artery in the neck. These cells can detect changes in carbon dioxide and oxygen levels (1). The sensory fibers coming from the muscles have also been shown to influence respiration (2). Further, pioneering studies performed in the 1980s revealed that stimulation of the brain areas involved in the initiation of locomotion increased respiration. These increases were maintained even in paralyzed animals (3). Moreover, in humans, respiratory increases can occur before movement or when subjects simulate exercise mentally. This suggests that feedback from movement is not necessary and that connections within the central nervous system are responsible for the respiratory increases. However, because these connections were never identified, they could never be specifically blocked to assess their contribution to the respiratory changes related to exercise. This recently prompted some researchers to argue that central connections from supraspinal locomotor centers in the brainstem, the posterior part of the brain adjacent to the spinal cord, do not contribute significantly to the respiratory increases (4). In this study, we used the lamprey, a basal species of fish, as an experimental model to identify the central neural structures underlying the respiratory increases related to movement. We now confirm that central connections in the brainstem play a crucial role in the respiratory adjustments during movement, and we have identified the neurons involved.

The central nervous system of the lamprey is much smaller and less complex than that of mammals, but shows a very similar general organization. In addition, it can be entirely isolated from the organism (i.e., in vitro), thus providing an ideal opportunity to examine the role of specific populations of neurons while preserving intact the neural networks controlling motor behaviors such as respiration and locomotion. By using the lamprey preparation, we identified a population of brainstem neurons that link a locomotor area and the respiratory rhythm-generating area. We first showed that, as with other animal species, intact lampreys display respiratory increases in association with locomotion. Changes occur even before swimming begins. We then isolated the brainstem and upper spinal cord in vitro, thus removing feedback from the muscles, but keeping the neural networks controlling locomotion and respiration intact. Stimulation of the mesencephalic locomotor region (MLR), a brainstem region known to control locomotion, elicited marked increases in respiration. Furthermore, we found that removing the spinal cord and the lower brainstem (corresponding to the medulla oblongata of higher vertebrates) did not abolish the respiratory increases, suggesting that the connections responsible for increasing respiration are located more anterior in the brainstem, in a region corresponding to the pons and lower midbrain of higher vertebrates. We recorded from a specific group of neurons within the MLR and found that (i) these neurons were active in parallel to the brainstem networks that control locomotion and (ii) they connected directly to the brainstem areas that generate breathing movements. We also examined the activity of individual neurons in the respiratory rhythm-generating area and found that stimulation of the MLR produces a large excitation in these cells that depended on glutamate.
a neurotransmitter. These results show, at the single-cell level, a connection between a brain center controlling locomotion and another generating the respiratory rhythm.

Previous research has shown that multiple mechanisms might contribute to the respiratory increase during exercise, and an ongoing debate has centered on the relative contribution of each mechanism. Therefore, we addressed whether the dorsal MLR was needed for the respiratory increases associated with locomotion. A semi-intact preparation was used, in which the brainstem and rostral spinal cord were isolated in vitro and the tail of the animal was kept intact. Blocking the excitatory connections in the dorsal part of the MLR would have three possible outcomes: (i) locomotion would be slowed down with reduced respiratory increases, indicating that the dorsal MLR controls both respiration and locomotion; (ii) locomotion would be unaffected with a reduced respiratory increase, indicating that the dorsal MLR controls respiration specifically; or (iii) both locomotion and the increase in respiration would be unaffected, indicating that the dorsal MLR has other roles. We found that blocking excitatory transmission in the dorsal MLR considerably reduced the respiratory increases while leaving the locomotor movements unaffected. This confirms that a subset of neurons in the dorsal MLR is specifically involved in the respiratory increases associated with movement and exercise.

Our results indicate that the neural commands that control movements are accompanied by a parallel command sent to the respiratory rhythm-generating centers via a specific neural substrate in the brainstem (Fig. P1). Such a direct connection between locomotor and respiratory control centers could provide an advantage in terms of the speed and precision of the respiratory changes related to movement. We showed that, in our experimental conditions, a major part of the respiratory changes relies on a central command from the dorsal part of the MLR. However, other mechanisms might also contribute to fine tuning the respiratory adjustments to ongoing movements, and their relative contribution remains to be determined. Our study reveals a parallel control originating in the MLR for two classes of motor behaviors: those allowing individuals to move in their environment and those allowing oxygen and carbon dioxide homeostasis. This work also has clinical relevance because the MLR is now a target for deep brain stimulation in patients with Parkinson disease.