both the brain and its function, we think it could also influence the study of psychological development in significant ways. Similarly, importing the idea of homology from evolutionary biology into developmental psychology could help researchers conceptualize behavioral development in new and potentially informative ways. Taken together, the concepts of neural reuse and developmental homology could be used to further our understanding of brain development, psychological development, and the relationships between these phenomena.

Reuse of identified neurons in multiple neural circuits

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Abstract: The growing recognition by cognitive neuroscientists that areas of vertebrate brains may be reused for multiple purposes either functionally during development or during evolution echoes a similar realization made by neuroscientists working on invertebrates. Because of these animals' relatively more accessible nervous systems, neuronal reuse can be examined at the level of individual identified neurons and fully characterized neural circuits.

The principle of neural reuse is widespread within peripheral sensory and motor circuits in both vertebrates and invertebrates. Peripheral sensory circuits, such as those in the retina, extract and process information that is used in many behaviors. Indeed, the coding of visual scenes or odors requires that overlapping sets of sensory neurons are activated in response to different scenes or odors. Likewise, overlapping sets of premotor and motor neurons may be activated in disparate behaviors that require activation of overlapping sets of muscles.

The detailed characterization of invertebrate neurons and neural circuits has demonstrated that neurons can be reused to form neural circuits that perform multiple functions. One striking example comes from the stomatogastric ganglion (STG) of the crab *Cancer borealis*. The ∼30 neurons of the STG control rhythmic muscle activity involved in chewing and digestion of food – the gastric mill and pyloric rhythms, respectively. Individual identified neurons may contribute to the production of more than one rhythm. The VD neuron, for example, is involved in the generation of both the gastric mill and pyloric rhythms (Weimann & Marder 1994). Thus, the dynamic restructuring of neural circuits within the STG provides a clear example of the reuse of neurons for the production of different behaviors.

Reuse may also be found in neurons involved in learning and memory. In the pond snail (*Lymnea stagnalis*), the breathing rhythm is generated by three synaptically connected neurons that form a central pattern generator. One of these neurons, RPeD1, is also necessary for many aspects of learning and memory; and removing the RPeD1 cell body can prevent the formation or reconsolidation of long-term memories (Sangha et al. 2003). In honeybees (*Apis mellifera*), a single identified neuron (VUMmx1) in the suboesophageal ganglion mediates the reward pathway in associative olfactory learning, but this neuron has also been implicated in learning phenomena as diverse as second-order conditioning and blocking (Menzel 2009).

The above examples emphasize that within the adult nervous system neurons are reused for different functions; but as Anderson points out, neurons may also be reused during development.

One such example is the reuse of larval motor neurons in the adult nervous system of the tobacco hornworm moth (*Manduca sexta*). *Manduca* caterpillars, like those of all moths and butterflies, undergo a metamorphosis that involves restructuring of the nervous system. Motor neurons that innervate leg muscles in the caterpillar have been shown to remodel their axons and dendrites during metamorphosis before innervating newly developed leg muscles (Kent & Levine 1993). Memories can also be retained between larval and adult forms of insects, despite the remodeling of neural networks during metamorphosis. For example, adult fruit flies (*Drosophila melanogaster*) retain memories of odors associated with aversive stimuli formed as third instar larvae (Tully et al. 1994). Memory retention between developmental stages suggests that those elements of neural circuits that are the loci of these stored memories are reused in adult animals.

Anderson also suggests that neurons may be reused during evolution, acquiring novel functions and possibly losing their original function. Again, invertebrate neural networks provide examples of such reuse during evolution. In the desert locust (*Schistocerca gregaria*), more than 20 interneurons have been identified from the neural networks controlling the flight muscles. Some of these interneurons have homologues in abdominal neuromeres, which innervate segments that do not bare wings or contain motor neurons innervating flight muscles (Robertson et al. 1982). Yet, these interneurons can reset the flight rhythm in the locust, showing that despite their location they are components of the flight control machinery. Indeed, their role in the flight control circuitry may have influenced the structure of the insect ventral nerve cord (Niven et al. 2006). Robertson et al. (1982) have suggested that these interneurons are remnants of control circuits for ancestral appendages that have been lost.

Neural reuse may be more prevalent in invertebrate brains, especially those of insects, which contain relatively few neurons compared to those of many mammals. Many insects possess small brains that have been miniaturized during evolution (Beuthel et al. 2005). Their small size means that insects are under selective pressure to reduce energetic costs and brain size (Chittka & Niven 2009). Anderson suggests that energy minimization in the absence of behavioral constraints would promote the reduction of neural structures and, thereby, the reuse of neural substrates. The possibility of reusing neurons for different behaviors through the dynamic restructuring of neural circuits means that the consequences of miniaturization may not be as severe as is often assumed.

Anatomical modularity is clear within invertebrate nervous systems (e.g., Niven et al. 2006) but, as Anderson mentions, neural reuse may blur the boundaries between anatomical modules. Indeed, most behaviors involve sensory and motor circuits that are overlapping anatomically, and it seems unlikely that the majority of behaviors are localized entirely within specific anatomical modules. As discussed above, the locust neurons involved in wing control, which include examples of evolutionary reuse, are spread across six neuromeres although only two segments bear wings (Robertson et al. 1982). Indeed, even reflex arcs confined to a single neuromere can be modified by descending and local control, allowing the neurons to be reused in different behaviors (Burrows 1996). Anatomical modularity has been suggested to reduce the energy consumption of neural processing by reducing the length of relatively common local connections and increasing the length of relatively rare long-distance connections. Thus, although modularity may be beneficial for efficiency, it may be opposed by neural reuse, which may not minimize the lengths of connections within neural circuits. In small brains, the low number of neurons and the short distances of most connections may promote further functional reuse, even when some components of neural circuits are in different anatomical segments. Thus, in small brains there may be an increased prevalence of neural reuse.