Ephemeral connections for reaching and grasping

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Bonsai is a tree-cultivation technique that has a rich history, spanning thousands of years. The goal is to grow an aesthetically pleasing miniature tree in a pot environment. One problem faced by practitioners of this art form is that the taller branches that grow first tend to extend outwards, shading the lower parts of the tree. Thus, the inner buds and leaves are stunted due to a lack of access to sunlight. To solve this problem, practitioners use wire to temporarily reposition the taller branches downward, until the interior growth has matured. The wires are then removed, having served their function. Similar temporary solutions are used during behavioral and neural development. Human infants exhibit a rooting reflex when their cheeks are stroked, turning their heads and opening their mouths in the direction of the stimulation. This is a behavioral adaptation for nursing that disappears as infants get older and no longer need it (1). Similarly, in the developing neocortex, subplate neurons form a temporary layer, keeping the early arriving connections from the thalamus viable until their permanent target—cortical layer 4—is formed; when that occurs, subplate neurons die off (2). In a study of marmoset monkeys, Mundinano et al. (3) share a similar story that links a temporary neural scaffolding with the proper development of an adaptive behavior.

Marmoset monkeys, like other primates, are able to deftly grasp objects through visually guided action of the hands. To do so, they use a complex network of brain regions (4). A key node in this network is a visual motion-sensitive cortical area known as the middle temporal area (or area MT). In adults, area MT receives visual signals primarily from a part of the thalamus known as the lateral geniculate nucleus that in turn gets its signals directly from the eye. The signal from area MT is then sent to a region known as the posterior parietal cortex that is critical for using visual information to guide hand actions (4). During development, however, the pattern of connections starts out a bit differently. In marmoset infants, visual information from the eye goes to a different part of the thalamus, known as the pulvinar, and then to area MT. Over some months, the pathway from the pulvinar to area MT diminishes, while the one from the geniculate strengthens (5). The key question is this: Does this temporary pathway from the pulvinar to area MT serve some function during development (e.g., keeping connections from the eye viable while the later-developing geniculate emerges), or is it just a nonadaptive "wiring error" that gets corrected [as seems to occur in other developing cortical pathways (6)]?

Is the Transient Pulvinar–Area MT Pathway Scaffolding for Subsequent Motor Development?

To get at the answer, Mundinano et al. (3) eliminated the pathway from the pulvinar to area MT during development and measured its consequences via a tour-de-force of approaches. First, the authors wanted to know whether knocking out this pathway on one side of the brain, via unilateral lesions of the pulvinar, would lead to motor behavior deficits when those infants grew to adulthood. The intact brain hemisphere and pathways therein could be used as controls. To assess this, Mundinano et al. developed a reaching and grasping task where marmosets needed to make visually guided hand movements. To do so typically involves the coordinated activity of several parts of the posterior parietal cortex as they receive visual signals from area MT. If behavioral deficits are apparent, then the logical next step was to see if this is because there are changes in the structure of the posterior parietal cortex. Diffusion tensor imaging (DTI) was used to measure any such change. This is a powerful method because it is noninvasive and thus can be used to collect longitudinal data. To get a more detailed picture of any neuroanatomical changes, Mundinano et al. (3) injected tracers in area MT after the animals grew to adulthood and examined how its connections to the posterior parietal cortex may have changed as a function of the pulvinar lesion. Finally, the authors hypothesized that the activity in the temporary pulvinar–area MT pathway may help spur the development of

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Author contributions: D.A.L. and A.A.G. wrote the paper.

The authors declare no conflict of interest.

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neurons in the posterior parietal cortex. Thus, Mundinano et al. used biochemical markers to identify which groups of neurons were mature or not.

The results were unequivocal. The lesions revealed that the transient pulvinar–area MT pathway is necessary for the proper development of visually guided reaching. Deficits in reaching parameters, such as the acceleration of the hand toward a graspable object, and the deceleration just before grasping it, were evident. Mundinano et al. (3) also measured "preshaping," the process of adapting one's hand shape to suit the contours of the grasp target. Relative to controls, the lesioned pathways resulted in adult marmosets producing grips that were maladaptive, larger than necessary for the object [a behavior similar to those exhibited by patients with optic ataxia (7)]. Linking the behavioral deficits to neuronal ones, the DTI experiments revealed reduced connectivity in the posterior parietal cortex in the lesioned hemisphere of the brain compared with the other, intact side. This diminished connectivity was echoed by the tract-tracing results, which revealed a reduction in the connections between area MT and the posterior parietal cortex. Finally, staining for biochemical markers of neuronal maturation showed fewer mature neurons in area MT and the posterior parietal cortex on the lesioned side, supporting the hypothesis that, early in life, visual signals in the transient pulvinar–area MT pathway push the development of both MT and its targets.

The Role of Ontogenetic Adaptations in Neural Development

Beyond its importance for understanding the mechanisms underlying the development of reaching and grasping behavior, this study illuminates an often-neglected but important phenomena in both development and evolution. Mundinano et al.'s (3) findings remind us that neural and behavioral development—like all biological development—is not just a gradual, progressive, and continuous accumulation of connections and adaptations; it also features transitions, losses, and regressions as it proceeds (8). Mundinano et al.'s (3) study also provides a particularly salient example of an ontogenetic adaptation. It is often overlooked that, on the way to becoming a mature individual, an organism must still be adapted to whatever conditions it encounters on the way to adulthood. Ontogenetic adaptations are those features or processes that are adaptively suitable at a particular age but which may be unnecessary or incompatible later on (8). The transient pathway between the pulvinar and area MT is just such an example, one whose importance is apparent at both the neural and behavioral levels (3).

Visually guided hand action is thought to be among the key adaptations of primates, enabling the reaching and grasping of not just branches while locomoting in the trees but also for grabbing fruits and insects (9). Its advent overlaps with the evolutionary expansions of the pulvinar nucleus and area MT, along with the latter's connections with the posterior parietal cortex (4). Thus, the transient pulvinar–area MT pathway is an ontogenetic adaptation that may have ultimately facilitated the evolution of visually guided reaching and grasping. A clearer understanding of how the evolution of such ontogenetic adaptations could lead to phylogenetic adaptations will require not only more comparative developmental studies, but also consideration of how changes in the body [e.g., the hand and its biomechanics (10)] influence neural and behavioral change. For example, the parallel evolution of cortical areas for proprioception and motor planning present in only one New World monkey species, compared with all Old World monkeys, is due partly through changes in hand biomechanics and the behavior that it facilitates (the precision grip) (11).

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Finally, it is worth noting yet another remarkable aspect of biological development and the role played by ontogenetic adaptations. While transient pathways like the pulvinar–area MT connection function like the wire used to guide Bonsai tree growth or the scaffolding around a house being built, neural and behavioral development are otherwise fundamentally very different. Man-made constructions involve a blueprint in the mind of an artist or on the drawings by an architect. They require an external agent directing the action according to a preconceived plan. The construction of an organism is nothing like this. It involves no blueprint. An organism's brain and body are being developed by the organism itself, with the added constraint that it must stay alive, generating adaptive behavior appropriate for each and every life-history stage.

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