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A computational model of anterior intraparietal (AIP) neurons

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Abstract

The monkey parietal anterior intraparietal area (AIP) is part of the grasp planning and execution circuit which contains neurons that encode object features relevant for grasping, such as the width and the height. In this study we focus on the formation of AIP neurons during grasp development. We propose and implement a neural network structure and a learning mechanism that is driven by successful grasp experiences during early grasp development. The simulations show that learning leads to emergence of units that have similar response properties as the AIP visual-dominant neurons. The results may have certain implications for the function of AIP neurons and thus should stimulate new experiments that cannot only verify/falsify the model but also advance our understanding of the visuomotor learning mechanisms employed by the primate brain.

Keywords: Anterior intraparietal area; Grasp learning; Affordance; Visuomotor development

1. Introduction

Humans visually monitor critical kinematic events for detecting errors in goal-directed movement execution [8] including grasping movements that require cortical integration of visual and somatosensory cues for proper grip formation [6]. The accumulated neurophysiological data indicate that the parietal cortex is involved in visuomotor aspects of manual manipulative movements [19]. In particular, the neurons in anterior intraparietal (AIP) area of macaque monkeys discharge in response to viewing and/or grasping of three-dimensional objects representing object features relevant for grasping [14,16]. Generally, AIP neurons are classified as one of motor-dominant (active during grasping, even in the dark), visual-motor, and visual-dominant (no movement is necessary; sole object fixation elicits response) types. AIP has strong recurrent connection with area F5 (ventral premotor cortex) [10] that is involved in grasp planning and execution [13], and projects to motoneurons that control finger muscles [2]. The activity of neurons in the primary motor cortex (F1) when compared to premotor activity indicates that the primary motor cortex may be more involved in dynamic aspects of movement [18], executing ‘instructions’ sent by higher motor centers including premotor regions. Thus, it has been suggested that AIP–F5–F1 circuit is responsible for grasp planning and execution [3–5,7]. However the formation/adaptation of the neural circuitry that extracts object features required for dexterous manipulation (i.e. AIP) is yet to be understood. To this end, it is important to know whether AIP representation is the final step of a series of visual analysis or the by product of the grasp-related visuo-motor learning.

In this article, we present a model of AIP visual-dominant neurons consistent with monkey grasping circuit that extends upon our earlier modeling of infant grasp learning (when we use AIP, we mean AIP visual-dominant from now on). Infant motor development studies have shown that during early grasping period of 4–6 months, infants do not use vision to guide hand trajectory or to orient the hand toward the object prior to initial contact.

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For example, at 4–5 months, reaches are as good with vision available during the reach as when vision is removed after onset of the reach [1]. Only after 9 months of age the visual features of the objects that are relevant for grasping (orientation, size, etc.) are incorporated into the grasping actions. This developmental progression suggests that earlier grasp learning may mediate the formation of a stronger grasp planning circuit that fully utilizes the visual information available. The model we present addresses the latter portion of this progression, where the less-visually guided grasp experiences provide (learning) data points for an infant's grasp related visuo-motor mapping system.

2. The model

2.1. Behavioral setting

The model we present addresses the developmental stage of 4–9 months where a basic grasping skill has been acquired. We present the model in terms of brain areas belonging to macaque monkeys, however, the developmental data is mainly from humans due to the lack of infant studies on other primates. In other words, we implicitly assume that the developmental aspects of the grasp circuit in humans and other primates follow similar stages.

The grounding assumption of the modeling presented in this article is that during early grasp learning infants associate the vision of the objects with the grasp plan (the motor code generating the grasp) that provides a stable grasping.

2.2. The systems level organization

We abstract the primate grasping circuit as shown in Fig. 1A. The visual input arriving to AIP—although processed at earlier visual areas—is void of geometric information about the object in the visual field. The task of AIP–F5 complex is then to transform the visual input into a motor code which when executed yields a successful (stable) grasping of the object. In the primates, the input to AIP is highly processed as there are multiple relay stations on the way from primary visual cortex to AIP. Nevertheless, these areas do not compute information such as width and height of the object in the visual field. To our knowledge, AIP and caudal intraparietal sulcus (cIPS) are the sole areas reported to encode geometric object properties. cIPS neurons encode orientation or axis of objects and may provide information for AIP [15]. For simplicity we do not model cIPS explicitly as a separate layer. However, we do expect to see units similar to cIPS neurons as well in our AIP layer (in spite of the naming). For this article, we focus only on the properties of unit responses that are comparable to AIP-like responses.

2.3. Input and output encoding

To capture the non-specificity of the visual input (i.e. lack of geometric information coding) we implemented the input to AIP as a depth encoding 'retina'. The visual processing taking place prior to AIP includes stereopsis, so this choice is justified by the monkey neurophysiology [15]. The most notable point of our representation is that it does not include any high level features extracted by a preprocessing step; what the network sees is just a depth map (i.e. matrix of real numbers). Notice that instead of an explicit depth encoding it is also possible to use two intensity coding retinas corresponding to two eyes, in which case we would predict the emergence of binocular neurons in the hidden layers. Since the depth encoding retina chosen for computational convenience does not contain more information than the two retina system (given the simple objects we used) the validity of the arguments we might draw from the model is not weakened by our choice.

For the motor code (F5) output we used joint angles of the fingers. Although the motor code in the brain must address dynamics and intrinsic properties of the muscles and lower motor control centers we believe the output code used does not limit the validity of the conclusions we can draw from the model.

2.4. Adaptation mechanism

The problem an infant faces during grasp learning is computationally stated as to learn the mapping from visual ($\vec{V}$) to motor codes ($\vec{G}$) that yield successful grasping. Notice that the learning mentioned here is only possible with the active movements of an infant, although the resulting neural structure may exhibit purely visual responses not requiring movement. The infant experiences many $\{\vec{V}_i, \vec{G}_i\}$ pairs during early grasping. At first, this problem seems to assume a simple function approximation solution, however, the mapping is not well defined: we can apply different grasps to a given object. Conversely, different objects can serve as the target for the very same grasp. The problem can be approached from several directions. One way is to model the association learning as learning the joint probability distribution $p(\vec{V}, \vec{G})$ of the visual representation of the object and the motor command. In this study we chose a more biological approach and propose a neural circuit with explicit neural units that can solve the problem: we propose that AIP–F5 complex consists of sub-networks (columns) that compete in the motor code space for being the one to learn the current $\{\vec{V}_i, \vec{G}_i\}$ (successful grasp association) pair (see Fig. 1B). The competition is implemented using a Kohonen's topology preserving self-organizing map (SOM). When a grasping attempt results in successful holding of the target object, the competition picks a sub-network to learn the current observed vision→motor association. Although other alternatives were possible, the learning in