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Attention flexibly alters tuning for object categories

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Abstract

Using functional MRI (fMRI) and a sophisticated forward encoding and decoding approach across the cortical surface, a new study examines how attention alternates tuning functions across a large set of semantic categories. The results suggest a dynamic attention mechanism that allocates greater resources to the attended and related semantic categories at the expense of unattended ones.

Natural environments contain many objects that cannot all be processed simultaneously due to capacity limitations of the visual system. Therefore, flexible mechanisms are needed to selectively prioritize information that is relevant to ongoing behavior at the expense of irrelevant distracting information. This selection process is often referred to as 'attention'. A variety of attention-related modulatory effects on neural processing across the visual system have been demonstrated, such as increases in baseline activity [1], increases in response gain of neurons that selectively respond to an attended feature or location [2,3], as well as shifts of neuronal tuning curves, for example, changes in preferred feature selectivity [4]. Although these studies have shaped initial understanding of attention, they have been limited to examining neural responses evoked predominantly by synthetic stimuli, such as gratings or oriented bars, which have been shown to elicit different response patterns than those obtained during natural vision [4,5]. It is not yet clear whether attention mechanisms revealed using synthetic stimuli generalize to a more complex, but ecologically valid context that is characteristic for natural vision, such as looking for a car when crossing a street. Recent fMRI studies have begun to examine the neural basis of attentional selection used in naturalistic vision by probing subjects' performance in tasks that involve categorical detection of objects embedded in scenes [6-8]. These studies have demonstrated that category-based attention biases the processing of an attended target stimulus category, even in the absence of visual stimulation [7], which facilitates and predicts behavioral search performance to the attended target category [7,8]. However, the category space probed thus far has been restricted to a small set of objects, which does not lend to the vast number of objects that people are able to recognize and discriminate in daily life. How do attentional mechanisms operate across the representations that constitute the large object space that people are able to perceive?

Kim and Kastner Page 2

A new fMRI study by Cukur and colleagues [9] utilizes a recently reported continuously mapped semantic space of a large (~1000) set of object and action categories across the whole brain [10] to investigate how attention mechanisms operate on such a large object space during naturalistic visual conditions. First, using a forward modeling approach, a category tuning function was estimated for each individual voxel (a volumetric unit of fMRI measurement), while subjects passively viewed natural movies. A single voxel measures a small portion of cortex at the millimeter scale. As a voxel contains many thousands of neurons with varying response properties, there are likely several different subpopulations of neurons that respond selectively to different semantic categories within this unit. A voxel's tuning function was estimated as the gradient of category selectivity across the large set of object categories for which the voxel's response could be most reliably predicted. Second, the modulations in voxel tunings were probed while subjects covertly attended to 'vehicles' or 'humans' in a movie search task. Attending to a particular category, say humans, shifted the category representations across a large proportion of cortical voxels distributed across the brain towards the 'human' representation, even in the absence of the target object. This change in category representation was observed for voxels that were initially tuned to the semantically related categories (e. g., representations for 'body parts' and 'animals' became more 'human'-like), as well as for those voxels initially tuned to the unattended and semantically unrelated categories (e.g., representations of 'vehicles' became less 'vehicle'like). This finding strongly suggests that category-based attention alters the category selectivity of cortical voxels towards the behaviorally relevant category at the expense of unattended or behaviorally irrelevant categories. Thus category-based attention appears to orchestrate a large network of cortical representations and the results of this study highlight the flexible and adaptive nature of attentional modulations across the whole brain.

Because a voxel is not a biological, but rather a technical unit, a critical unresolved issue is to reveal the neural mechanisms by which the changes in category selectivity across object space are mediated. The authors argue that the observed modulations are a consequence of shifts in categorical tuning functions that are not related to an additive or multiplicative change of neural responses within a voxel. However, a tuning change at the voxel-level could be mediated by selective response gain operating differentially on subpopulations of neurons contained in a voxel. For example, consider a voxel composed of a large subpopulation of neurons tuned to humans and a small subpopulation of neurons tuned to vehicles. This voxel would be labeled as a human-preferring voxel. When attention is directed towards humans, a response gain of only those neurons tuned to humans and suppression of those neurons tuned to vehicles could manifest without necessarily changing the proportion of individual neurons' preference or selectivity for the human and vehicle categories. At the pooled-voxel level, however, these changes in response gain and suppression would be manifested as an expansion of the representation of the human (attended) category and compression of the vehicle (unattended) category, which could account for the observed findings without assuming a neural mechanism that does not necessarily alter the selectivity of neurons responding to a preferred object category. If however, the neural mechanisms that underlie voxel-wise tuning shifts were mediated by shifts at the neural level, this would imply that attention allows changeable neural selectivity that arises from varying behavioral goals.

Kim and Kastner Page 3

Cukur et al.'s findings provide evidence for a potential large-scale neural operation by which attention overcomes capacity limitations to prioritize processing of attended and conceptually-related categories. This study sets the stage for future research in several important ways. First, how does attention influence object category tunings when the object space itself is changing? Daily experience is such that visual representations are vastly adapted to contextual information both in terms of visuo-spatial context (e.g., the representation of vehicles when other semantically related objects are present vs when semantically unrelated objects are present) and temporal context (e. g., the representation of vehicles when attending to humans shortly after attending to vehicles vs after continually attending to humans). Second, what are the functional dissociations between different brain regions (e. g., sensory vs higher order cortex) that mediate the attentional modulations in category tuning functions? And finally, how do these changes relate to behavioral outcome? Given that a large proportion of the brain exhibits significant attentional tuning changes, it is highly unlikely that all of these areas have redundant functional roles. How distinct brain regions work collectively to achieve a common overarching goal and how this guides and relates to efficient behavioral performance, such as greater detection sensitivity or better memory for attended and semantically related objects, will be exciting questions for future research.

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