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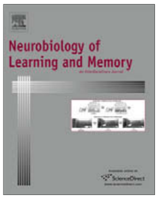

Parietal control of attentional guidance: The significance of sensory, motivational and motor factors

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ABSTRACT

The lateral intraparietal area (LIP), a portion of monkey posterior parietal cortex, has been implicated in spatial attention. We review recent evidence showing that LIP encodes a priority map of the external environment that specifies the momentary locus of attention and is activated in a variety of behavioral tasks. The priority map in LIP is shaped by task-specific motor, cognitive and motivational variables, the functional significance of which is not entirely understood. We suggest that these modulations represent teaching signals by which the brain learns to identify attentional priority of various stimuli based on the task-specific associations between these stimuli, the required action and expected outcome.

1. Introduction

Judicious selection is at the heart of goal directed behavior. To select appropriately in a complex environment an intelligent agent (be it a person, a rat or a monkey), must solve two problems. First, the agent must identify the most relevant source of information from among many potential alternatives. Second, it must be able to focus on the relevant source and block out irrelevant distractions. In both intuitive and scientific terms, we think of the cognitive operations that allow such adaptive selection as falling into the broad realm of "attention".

It is often claimed that attention is necessary for overcoming capacity limitations inherent in neural processing. Because the brain is "bombarded" with more sensory information than it can process in depth, the argument goes, attention is needed to prioritize and limit the amount of information that reaches higher processing stages at any one time. However, the need for selection remains even in simple environments that do not seriously tax capacity limitations. Even in such environments, we must decide which objects are helpful to us and which are not. The essence of attention is therefore the act of assigning credit, or *identifying* the sources of information that are most relevant in a given context. Generally this decision requires *learning* about the statistical contingencies between various objects, actions and outcomes. It follows that attention must be a dynamic selection mechanism that is exquisitely sensitive to immediate task demands.

Neurophysiological investigations in non-human primates have focused on three areas as being important for the control of attention: the frontal eye field in the frontal lobe, the superior colliculus in the midbrain, and the lateral intraparietal area (LIP) in the parietal cortex. In this review we describe the state of our knowledge about one node of this network, area LIP, which has been especially well investigated and provides an excellent model system for further inquiry into the mechanisms of attention. Investigations into LIP began with the somewhat naïve view that an area controlling attention must simply represent objects or locations that are attended at a given moment and respond relatively weakly to distractors. To a first approximation, this is indeed what is found in LIP. However, recent evidence shows that this "priority map" is more complex and in particular that it takes on a wide range of task-specific properties – i.e., it appears to be plastic and adaptable to task demands. The specific significance of these modulations is not fully understood. However, we suggest that these modulations represent teaching signals through which the brain learns to assign attentional priority to various stimuli based on their significance for a specific action or a specific outcome. We end by describing a computational model (Roelfsema & van Ooyen, 2005) that may be a good starting point for formalizing inquiry into the links between learning and attention.

2. Methods

2.1. General methods and behavioral tasks

Data were collected with standard behavioral and neurophysiological techniques as described previously (Balan & Gottlieb, 2006;

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Oristaglio, Schneider, Balan, & Gottlieb, 2006). All methods were approved by the Animal Care and Use Committees of Columbia University and New York State Psychiatric Institute as complying with the guidelines within the Public Health Service Guide for the Care and Use of Laboratory Animals. During experimental sessions monkeys sat in a primate chair with their heads were fixed in the straight ahead position. Visual stimuli were presented on a SONY GDM-FW9000 Trinitron monitor (30.8 by 48.2 cm viewing area) located 57 cm in front of the monkeys' eyes.

2.2. Identification of LIP

Structural MRI was used to verify that electrode tracks coursed through the lateral bank of the intraparietal sulcus. Before testing on the search task each neuron was first characterized with the memory saccade task on which, after the monkey fixated a central fixation point, a small annulus (1 deg diameter) was flashed for 100 ms at a peripheral location and, after a brief delay the monkey was rewarded for making a saccade to the remembered location of the annulus. All the neurons described here had significant spatial selectivity in the memory saccade task (1-way Kruskal–Wallis analysis of variance, $p < .05$) and virtually all (97%) showed this selectivity during the delay or presaccadic epochs (400–900 ms after target onset and 200 ms before saccade onset).

2.3. Covert search task

The basic variant of the covert search task (Fig. 2a) was tested with display size of four elements. Individual stimuli were scaled with retinal eccentricity and ranged from 1.5 to 3.0 deg in height and 1.0 to 2.0 deg in width. To begin a trial, monkeys fixated a central fixation spot (presented anew on each trial) and grabbed two response bars (Fig. 2). Two line elements were then removed from each placeholder, yielding a display with one cue (a right- or left-facing letter "E") and several unique distractors. Monkeys were rewarded for reporting cue orientation by releasing the right bar for a right-facing cue or the left bar for a left-facing cue within 100–1000 ms of the display change. A correct response was rewarded with a drop of juice, after which the fixation point was removed and the placeholder display was restored. Fixation was continuously enforced to within 1.5–2 deg of the fixation point. Errors (fixation breaks, incorrect, early or late bar releases) were aborted without reward.

In the perturbation version of the search task the initial fixation interval was lengthened to 800 or 1200 ms on each trial and a 50 ms perturbation was presented starting 200 ms before presentation of the target display. To increase task difficulty display size was increased to 12 elements and only a fraction of each line segment was removed from each placeholder. The location of perturbation and target were randomly selected from among a restricted neighborhood of 2 or 3 elements centered in and opposite the neuron's receptive field (RF), with a spatial relationship determined by behavioral context. Contexts were run in randomly interleaved blocks of ~300 trials. Within each context the location of target and perturbation and 2–3 of the possible perturbation types (see text) were randomly interleaved.

2.4. Data analysis

Firing rates were measured from the raw spike times and, unless otherwise stated, statistical tests are based on the Wilcoxon rank test or paired-rank test, or on non-parametric analysis of variance, evaluated at $p = .05$. For population analyses average firing rates were calculated for each neuron and the distributions of average firing rates were compared.

3. Results

3.1. Area LIP

In the rhesus monkey, where it has been most extensively characterized, the LIP occupies a small portion of the lateral bank of the intraparietal sulcus (Fig. 1). Although a homologue of LIP is thought to exist in human parietal cortex, no consensus yet exists about its location and functional profile. Anatomically, LIP is well situated to receive visual, motor, motivational and cognitive information. It has extensive anatomical connections with an oculomotor structure, the frontal eye field (FEF) in the frontal lobe, and weaker links with neighboring parietal areas that are related to skeletal (arm and hand) movements (Lewis & Van Essen, 2000a, 2000b; Nakamura et al., 2001). It projects to the superior colliculus, a subcortical oculomotor area. In addition, LIP has bi-directional connections with extrastriate visual areas including motion selective areas in the dorsal stream and shape and color selective areas in the ventral stream (Lewis & Van Essen, 2000b). Finally, LIP is reciprocally connected with the posterior cingulate, a limbic area, and with the perirhinal and parahippocampal cortex, which comprise the gateway to the hippocampus (Blatt, Andersen, & Stoner, 1990).

Consistent with their rich visual inputs, many LIP neurons have visual responses and spatial receptive fields (RF), which are typically contralateral to the recorded hemisphere and confined to a single quadrant (Ben Hamed, Duhamel, Bremmer, & Graf, 2001). Thus, the LIP in each hemisphere comprises a complete representation of the contralateral field with a rough topographic organization, that include a representation of the perifoveal region, (Ben Hamed et al., 2001). RFs are retinotopic – that is, they are linked to the retina and move in space each time the eye moves. However, neurons also receive extraretinal information regarding eye position and impending eye movements, which may be used to extract information in a more stable, world-referenced coordinate frames (Colby & Goldberg, 1999). Thus, the topographic representation in LIP is informed of the organism's position and is suitable for generating motor commands directed toward specific spatial locations.

In contrast with neurons in neighboring areas 7a or the ventral intraparietal area (VIP) that are best activated by large or full-field moving stimuli, LIP neurons respond exuberantly to small objects flashed inside their RF. Visual onset responses occur with latencies as short as 40 ms and are notable for their precision and reliability (Bisley, Krishna, & Goldberg, 2004). However, despite their machine-like quality, these visual responses are not mere "sensory transients" but report the physical salience (conspicuity) of the stimuli eliciting them. This has been shown in a task in which an array of stimuli remained stable on the screen, and monkeys made eye movements that brought these stimuli into the RF (Gottlieb, Kusunoki, & Goldberg, 1998). Neurons had little response to the stable, stimuli if these were not relevant to the task. Thus, complex, natural scenes evoke relatively little activity in LIP, but neurons selectively respond to intrinsically salient, flashed objects.

LIP responses to flashed stimuli correlate with automatic shifts of attention to salient objects. Bisley and Goldberg showed that the visual on response in LIP predicted the time course of rapid, covert attentional shifts toward a flashed distractor (Bisley & Goldberg, 2003). Balan and Gottlieb (Balan & Gottlieb, 2006) showed that neurons respond equally to visual transients defined by different physical characteristics, such as an abrupt change in color, position or luminance (Fig. 3a).

In addition to their sensitivity to stimulus-driven salience, neurons are also strongly sensitive to task-related factors. The earliest evidence for top-down modulations came from a study of Bushnell et al. who found that visual onset responses in LIP and in neighbor-