Facilitation, Inhibition, and the Advantage of Two Connections

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COMMENTARY ON: LaBerge, D. (1997) "Attention, Awareness, and the Triangular Circuit". *Consciousness and Cognition,* *6*, 149-181. (See also La Berge's precis for PSYCHE.)

1. Introduction

In recent discussions on consciousness among researchers in cognition and neuroscience, one recurring theme is that consciousness requires not just activity in one specific part of the brain, but coordinated activity across different brain regions that are far apart. In this article, LaBerge makes few claims about consciousness; instead he focuses on the related but somewhat better defined ideas of awareness and attention. However, he does adopt the same basic assumptions that these functions require coordinated activity across far-flung brain regions. He considers the brain areas that are involved in awareness and attention, and the nature of the connections linking these areas.

LaBerge integrates a number of relevant results from neuroscience and cognitive science, and many of his points can be examined and explored in detail. In this commentary I will start by exploring exactly what is being explained, then move on to details about the nature of the connections that LaBerge is proposing, and end by noting some possible relationships between his account of excitation and inhibition in attentional selection and some other recent experimental results.

2. Is This the Whole Story of Attention?

Crick and Koch (1990) warn about the dangers of becoming bogged down in trying to define consciousness, and the same could be said for the concepts of attention and awareness as well. Many of us who study attention accept William James' (1890) point that "every one knows what attention is" and do not bother to define it. However, despite the fact that we all use the same term "attention," we are often referring to very different types of mental processes. After James declared that we all know what attention is, he nonetheless went on to explain what he meant when he referred to attention. As our theories and models become more specific, it is important for us to do the same.

LaBerge clearly states that he believes prefrontal areas control what information is selected by attention. If these prefrontal structures are responsible for all decisions about attentional selection, then they are very busy areas. Given the huge amount of information available through all of the sensory modalities at any given moment, and the speed with which attentional selection is accomplished, these frontal regions will be heavily burdened if they must make all the decisions themselves.

Luckily for the frontal lobes, much of the work of attentional selection can be performed by lower-level mechanisms. Many models of visual attention have demonstrated that effective visual selection is often possible using only simple visual features such as color and orientation that are identified early in visual processing (e.g. Treisman & Gelade, 1980; Cave & Wolfe, 1990; Cave, in press). Once the features to be sought have been specified by a high level mechanism (perhaps in the prefrontal regions LaBerge describes), much of the work can be accomplished by simple comparison operations that can be performed in the posterior visual areas without information moving to and from the frontal lobes.

When LaBerge refers to attention in this paper, I take him to be referring to the highest level of selection in the brain, and his ideas about the interaction between prefrontal cortex, the thalamus, and other brain regions in this selection process are quite interesting. I assume, and I expect he does too, that the prefrontal areas are selecting from information that is the product of other, lower-level selection processes performed by more local connections with little interaction from prefrontal cortex.

3. Awareness, Self-awareness, and Verbal Report

Although there is plenty of ambiguity surrounding different conceptions of attention, there is even more ambiguity around the idea of awareness. LaBerge offers his own unique criterion for awareness: awareness can only occur with the involvement of the mental representation of the self. LaBerge's motivation for this claim is not clear. Is he saying that all mental activity that we associate with awareness requires activation of the self representation? My introspections, for what they are worth, suggest otherwise. Recall the last time you were at a movie and became totally engrossed in the story. You forget where you are, what time it is, and what is happening anywhere except on the screen. No sensory input receives any attention other than the sight and sound of the movie. You are too involved in the action on screen to remember to eat your popcorn. It seems that your representation of self would be taking a rest during this time, but how would LaBerge explain the situation? Would he say that despite the fact that everything about yourself seems to be excluded from your thoughts, that your self representation is still integrally involved? Or would he claim that you are simply "unaware" during this time?

In the last two paragraphs before the General Summary, LaBerge indicates that he would choose the latter explanation. He would describe your state in the movie theater as one of heightened attention to the movie, but not awareness. He does point out that what he describes as mere attention would be described by others as awareness, and what he describes as awareness would be described by others as self-awareness. I am not sure, however, why he chooses these particular terms. His terminology leads to an odd situation: After the movie, if I ask you about the story, you will be able to recount it in great detail. You will be giving a detailed verbal account of something that you were completely "unaware" of, according to LaBerge.

At the same time that LaBerge's definition emphasizes the role of the self-representation, it de-emphasizes the distinction between mental processes that we can report and those that we cannot. This distinction is at the core of many definitions of awareness, and I am curious why it is less important in LaBerge's account. LaBerge must have some strong motivation for redefining these terms in this counterintuitive way. Perhaps he wants to stress an important difference he sees between cognitive processes affected by the self-representation and those that are not. I hope he will explain his thinking about awareness more fully.

4. The Value of Two Connections

LaBerge proposes a triangular circuit as a basic mechanism for linking simultaneous activity across different brain areas. He offers two examples of how these triangular connections can work. The first example is centered around activation traveling from area V1 to area V2. In Figure 4 [Figure 3 in the precis], this circuit is shown as a purely feedforward connection. As Figure 4 shows, information can travel either by a direct connection from V1 to V2, or by an indirect connection that passes through the thalamus.

Why are two different connections necessary between V1 and V2 (or between any pair of the brain regions shown in Figure 4)? LaBerge explains (p. 161) that the thalamic connection can have a large effect on the strength of the input coming into V2. It serves as an amplifier for small activity differences in V1. LaBerge compares this part of the circuit to the control panels at a power plant. Like the signals coming in and out of the control panels, the signals in V1 can be very small, but they can control the flow of large amounts of power in some distant structure, such as the thalamus.

However, if this logic explains why the thalamic part of the circuit is necessary, it does not explain why the direct connection is necessary. If V1 can exert powerful and precise control over V2 through the thalamus, why should it have a direct connection at all? Is the direct connection an evolutionary precursor of the thalamic connection that is no longer really necessary? Are the two connections carrying different information and connecting to different substructures within V2? Does the extra speed that comes with the direct connection play a special part in the initial activation of V2? LaBerge notes studies such as Moran and Desimone's (1985) that suggest there is an initial burst of neural activity that is then tempered by selection processes. Perhaps the initial burst is produced by the direct connection, and the selectional shaping of the activity comes through the thalamic connection.

The second example of a triangular circuit connects brain regions that are more widely separated. A prefrontal control area has two connections to a high-level visual area in the temporal lobe: one is direct and the other is routed through the thalamus. Here we can again ask why two connections are necessary, but in this case there is a subtle but potentially important difference between Figures 4 and 5. Figure 4 shows only a one-way connection between V1 and V2, suggesting that the feedback connections from V2 to V1 do not play a major role in LaBerge's account. In Figure 5, however, the connection between the precortical and temporal areas is clearly a two-way connection. If the precortical area is serving as a control center, then the information flowing into it from the posterior sensory mechanisms is just as important as the information flowing back out. The need for a triangular circuit in this case is more apparent. The control center decides that it needs a particular type of sensory information, and sends the appropriate control signals to the thalamus. The thalamus exerts its strong influence on visual processing in the temporal lobe, which results in the desired information flowing from the temporal lobe back to the prefrontal control center. Signals travel around a continuous feedback loop, and the question arises whether there is any need for a direct connection carrying information from the prefrontal control area to the temporal area.

More importantly, This type of circuit seems very different from the feedforward circuit shown in Figure 4, in which all signals start and end at the same place after traveling along two different paths. Are these two circuits performing the same type of coordinating function, and should they really be classified as the same type of circuit?

5. Facilitation vs. Inhibition

There are some interesting parallels between recent evidence from attentional experiments in humans and LaBerge's observations about the roles of excitation and inhibition. As LaBerge points out, a target can be selected from among distractors by either facilitating processing of the target or by inhibiting processing of the distractors. Assumptions about the underlying neural implementation made from perceptual data can be dangerous, because either method of selection could in theory be implemented by either excitatory or inhibitory neural connections. In other words, even if the behavioral data showed a clear pattern of facilitation of the target over the rest of the visual input, that pattern could in theory be produced by neural connections that inhibit all inputs except the target. Despite these difficulties in linking the behavioral level and the neural level, there are some intriguing parallels between LaBerge's neural claims and recent behavioral evidence.

Some location cuing experiments (e.g., Downing & Pinker, 1985; LaBerge, 1983; LaBerge & Brown, 1989) show an attentional gradient, with attention being strongest at the target location, and falling off gradually with distance from the target. Because this gradient pattern is centered on the target location, it strongly suggests selection by target facilitation rather than distractor inhibition. However, in a different sort of attentional task, in which the target was designated by color rather than location, we found clear evidence for inhibition of distractor locations (Cepeda, Cave, Bichot, & Kim, 1998). In our experiment, subjects searched for a target of one color in an array of distractors of another color. The search array was followed by a spatial probe. Detection of the probe was fast when it appeared at the target location OR the background regions between display elements, but it was slow when the probe appeared at a distractor location. Because the attentional effects were focused mainly on the distractor locations without spreading much to the regions around the distractors, this pattern strongly suggests that subjects search for a target of a particular color by specifically inhibiting locations with another color. The assumption that attention works by distractor inhibition in these searches makes it easier to explain the flanking inhibition found by Cave and Zimmerman (1997), in which distractors near a target are more inhibited than distractors farther from the target. Distractor inhibition also provides a simple explanation for recent evidence that two target locations can be selected simultaneously (Kramer & Hahn, 1995; Bichot, Cave, & Pashler, in press).

When we designed a neural network model to account for the behavioral data, we were able to wire up the system in a straightforward manner without any long-range inhibitory connections (Cave, in press; Cave, Kim, Bichot, & Sobel, 1998). In this model, which we named FeatureGate, location cueing and color search rely on two different mechanisms, which produce very different patterns of attention. When a target location is cued, a high-level control center (perhaps LaBerge's prefrontal region, or perhaps some other center) interprets the cue and directly activates those parts of the relevant visual areas with receptive fields in the cued region, using long-range excitatory connections. Because of the hierarchical structure of our neural net, this activation produces a gradient of attention centered on the target location. However, when the target is defined by color rather than location, as in Cepeda et al.'s color searches, then selection is more complicated. The attentional system must first find locations with target or distractor colors, and then operate on those locations accordingly. We claim that in this task the control center merely sends a message to the visual areas specifying target and distractor colors. The hard work is done by local networks within the visual areas that compare colors at neighboring locations and inhibit distractor-color locations when target-color locations are present. Because this inhibition is generated by local mechanisms, it is also consistent with LaBerge's observations. Thus, our modeling has led to a conclusion similar to LaBerge's: visual selection can be implemented without long-range inhibitory connections.

The FeatureGate model simulates selection by location, and currently it does not address location-independent negative priming. In an earlier commentary, Cowan argued that negative priming probably relies on long-range inhibitory connections. Cowan's point deserves serious consideration, but there may be ways to implement negative priming with short-range inhibitory connections. Long-range connections would be required if negative priming occurs completely within a neural representation that is organized spatially, so that the distractor may be represented by neurons far removed from those representing the target. However, this type of negative priming might be controlled at a higher level in which representations are organized according to properties other than location, with similar items being represented near each other. Since the distractors and targets in negative priming experiments often share many properties, they will often be represented near one another, and the connections implementing the inhibition could be short.

There are many questions to be answered and potential conflicts to be resolved between LaBerge's account and some of the experimental data. For instance, in our color search experiments the inhibition was fairly tightly focused around the distractor location, yet each distractor was some distance away from the target. The connections necessary to implement this inhibition do not need to be extremely long, but they will need to extend beyond the range of an individual receptive field, contrary to LaBerge's observations. Despite details such as this, the general method of selection suggested by the data described above fits LaBerge's account well enough to merit further examination.

6. Summary

In this paper, LaBerge provides a collection of intriguing ideas to get us started in the examination of interactions across brain regions that result in attentional selection and awareness. Measuring and interpreting these interactions is likely to be difficult, but it will be somewhat easier if he is correct in his claim that the same basic triangular circuit appears repeatedly in connections across brain regions. I am curious to hear more about the advantages he sees for these circuits and the similarities he expects to find across the many different long-range connections that link different brain areas together.

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