Neurons that know when to quit

Jeremy M Wolfe

With sufficient training, monkeys as well as people can be taught to ignore visually salient stimuli. Now Ipata and colleagues report that activity in monkey lateral intraparietal cortex (LIP) correlates with this ability to ignore salient stimuli, suggesting that activity in this area represents top-down modulation that adjusts visual salience.

In Euripides' play *Helen*, a servant to the king of Egypt says, "Man's most valuable trait is a judicious sense of what not to believe." He wasn't talking about visual attention at the time, but an ability to ignore misleading information is vital to the successful deployment of spatial attention. In this issue, Ipata and colleagues[1] report on activity in neurons of the lateral interparietal area (LIP) of macaque cortex that corresponds to this ability. They taught macaque monkeys to identify the orientation of a T in a field containing a number of crosses. The monkey needed to find the T and then make a response indicating its orientation. Critically, for this experiment, the visual displays contained a uniquely colored, attention-grabbing item that was never the T. The visual system is built to respond strongly to salient colored stimuli. Such color singletons are said to 'pop out' of a display[2]. All else being equal, they will summon attention. However, because the uniquely colored item was never the target, Ipata's judicious monkeys learned not to believe that item when it screamed, "Attend to me," and the monkeys' LIP neurons learned to actively suppress their response to what would have otherwise been a very stimulating stimulus. After training, responses to the pop-out singleton were actually lower than responses to other distractors in the display.

Ipata *et al.* measured the tendency of the color singleton to grab attention by monitoring the monkeys' eye movements. In training, when the color oddball could be the target, monkeys made a saccadic eye movement to that odd item on nearly every trial. When the rules were changed so that the singleton was never the target, the number of saccades to that item dropped dramatically. Like human observers, monkeys were not perfectly consistent in their behavior, and this provided an added piece of evidence that the behavior of LIP neurons was related to the behavior of the whole organism. Sometimes the monkeys returned to making frequent saccades to the singleton even though it was never the target. During those periods, their LIP neurons again showed a stronger response to the singleton than to other stimuli. This was true even when the monkey made a saccade away from the singleton, showing that the strong response was not related to the planning or execution of the eye movement.

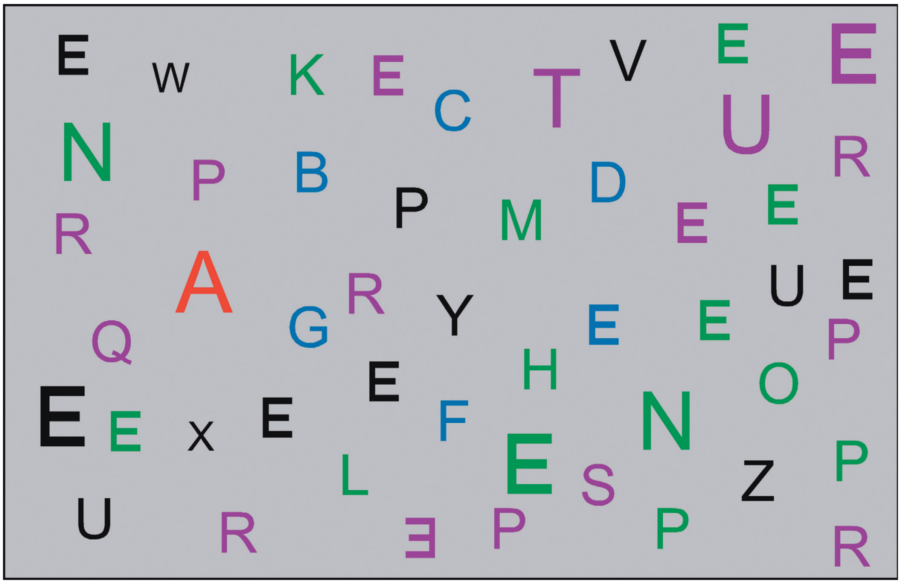

Figure 1 That red A grabs your attention, but does it have to? Cells in macaque lateral interparietal area can suppress their normal response to a salient stimulus like this if it is misleading.

To see why this ability to suppress response to a salient stimulus is important, look at **Figure 1**. The visual system cannot fully process everything everywhere in a single step. Visual selective attention is part of the response to this computational reality. If you want to identify letters, attention needs to be deployed to one or perhaps a few letters at a time. That deployment is controlled by a combination of top-down and bottom-up factors.

On first glance, that red A probably grabbed your attention. Bottom-up, stimulus-driven mechanisms guide attention to items that are dramatically different from their neighbors[3]. If bottom-up salience were the end of the story, you would be the slave of the stimulus. Instead, you are able to impose top-down, user-driven control, allowing you to modify your impression of this image without changing the stimulus itself. For example, attend to the blue items. As you do this, you may notice that the red A, while not vanish-

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ing, makes less of a demand on your attention. The blues, in contrast, now seem more salient. You may now notice that they form a rough circle. Moreover, having somehow taken note of the whole set, you can now direct your attention to individual blue items and notice that they consist of the letters B through G in clockwise order.

Notice that there are two steps involved here. The top-down command to favor blue items changes the effective salience of all blue items. Object identification mechanisms can then select individual items within the blue set. The Ipata results pertain to the first step. Response to the color singleton is suppressed so that it is almost never a candidate for the second selective step. The distinction can be illustrated by returning to the figure to search for the S and for the black P. You will probably find that you are faster to find the black P because that first, guiding step can be used to eliminate letters that are not black[4].

If the first step were sufficiently powerful, the second step would not be necessary. Thus, in the Ipata task, if the monkeys could just teach LIP to suppress all of the crosses, then attention would be deployed to the T, first time, every time. That will not happen because the abilities of that first stage are quite limited[5]. Returning again to the figure, are any of the Es mirror-reversed? Of course, you can find the one mirror-reversed E, but you will need to search. No top-down command will give you the entire set of Es in the same, seemingly effortless manner in which the blue or black sets were delivered to you.

So, salient stimuli will grab your attention in a bottom-up manner, but top-down control allows you to avoid perseverating on the one or two hot spots in a scene. Are there stimuli that are so salient that they will grab your attention regardless of any top-down desires or commands? This is the problem of attentional capture. Fortunately, the answer to the strongest form of this question is almost undoubtedly "no." If there were a visual stimulus so salient that it would grab attention and never let go, advertisers would have us glued to it. The more reasonable question is whether there are stimuli that attract attention in a mandatory fashion even if we are subsequently released to attend elsewhere. A variety of stimuli have been suggested to have the ability to capture attention in this way. For example, luminance onsets have proven more successful than our color singleton in forcing attentional deployment. It may not be simple luminance but the appearance of a new object that is particularly effective[6], though others disagree[7]. Moreover, it is possible that attentional capture occurs only if you are in a state where you are, in a sense, ready to be captured (so-called 'contingent capture')[8].

Opinion varies about the mandatory nature of attentional capture. The Ipata results would seem to lend support to the nonmandatory side, to the argument that it is possible to put in place a top-down filter that allows you to successful ignore a salient stimulus. However, as noted above, there are stimuli that may have a greater ability to capture attention than the color singletons used in this study. Both top-down and bottom-up components of attentional guidance are powerful. Sufficiently strong task demands can produce attentional 'tunnel vision' where everything but the attended item seems blocked out[9,10] but, in the end, the 19th century writer Sully had a fair point when he said, "One would like to know the fortunate (or unfortunate) man who could receive a box on the ear and not attend to it"[11].

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BK channels and circadian output

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The suprachiasmatic nucleus (SCN) controls circadian behavior, and neurons in the SCN are intrinsic oscillators. Meredith *et al.* now identify the BK potassium channel as a key modulator of spontaneous firing of the SCN.

You are lying in your bed, staring at the ceiling, waiting for sleep to come your way and wondering why it has become so difficult to find. Among other reasons, these sleepless nights are caused by our circadian timing system turning on arousal centers in our brain at inappropriate times. This problem may be particularly common during the summer travel season when we are jetting off to attend a conference or perhaps to catch a World Cup match. Would it not be nice to be able to turn down this biological timing signal, if only for a few days while we adjust to new time zones? New research in this issue by Meredith and colleagues into the ionic mechanisms underlying circadian oscillations may well open up the prospect for such manipulations in the future[1].

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Humans and other organisms have daily rhythms in their behavior and physiology. In mammals, the part of the nervous system responsible for most circadian behavior is a bilaterally paired structure in the hypothalamus, the SCN. Many neurons in the SCN are intrinsic oscillators that continue to generate near 24-hour rhythms in electrical activity, secretion and gene expression when isolated from the rest of the organism. Individual SCN neurons contain a molecular feedback loop that drives these rhythms. However, membrane excitability and/or synaptic transmission may also be required for generation of the molecular oscillations. For example, disruption of electrical activity with tetrodotoxin (TTX) damps molecular circadian rhythms of *mPer1* levels in SCN tissue[2]. A similar loss of function at the molecular level is observed in mice deficient in receptors for the neuropeptide transmitter vasoactive intestinal polypeptide[3]. Thus, clarifying the ionic mechanisms responsible for the generation of rhythms in electrical activity in SCN neurons is an important step for understanding the generation and output of circadian oscillations.

The new study by Meredith and colleagues takes a step in this direction by examining the role of the large-conductance calcium-activated potassium (BK) channels in circadian behavior[1]. With this work, the authors have