

## Journal Club

**Editor's Note:** These short reviews of a recent paper in the *Journal*, written exclusively by graduate students or postdoctoral fellows, are intended to mimic the journal clubs that exist in your own departments or institutions. For more information on the format and purpose of the Journal Club, please see [http://www.jneurosci.org/misc/ifa\\_features.shtml](http://www.jneurosci.org/misc/ifa_features.shtml).

## The Time Course of Shifting Visual Attention

Laura Busse and Steffen Katzner

Cognitive Neuroscience Laboratory, German Primate Center, 37707 Göttingen, Germany

Review of Khayat et al. (<http://www.jneurosci.org/cgi/content/full/26/1/138>)

At any instant, we are confronted with more information than we can fully process, because our sensory and cognitive resources are limited. To cope with this avalanche we use selective attention to enhance information from the environment that we care about and suppress the rest. Extracellular single-unit recordings in the visual cortex of awake, behaving macaques have provided detailed information about the mechanisms of “sustained” attention. In these studies, attention was directed to a visual stimulus or a stream of visual stimuli for up to several seconds. Little is known, though, about “shifts” in attention. This is an important gap in our knowledge because attention must operate on millisecond time scales. Imagine driving along a busy road. While keeping your eyes on the road, you also have to attend to cars on each side, pedestrians crossing the street, upcoming signs and changing traffic lights. In such a situation, accident-free driving is only possible because we are able to quickly shift our focus of attention, thereby temporarily “lightening up” representations of the most relevant objects in the visual scene.

A recent study by Khayat et al. (2006) in *The Journal of Neuroscience* (<http://www.jneurosci.org/cgi/content/full/26/1/138>) addresses how this might be achieved. The authors recorded multiunit

activity from the primary visual cortex (V1) in two macaque monkeys while the animals performed a variant of the “curve-tracking” task, an elegant paradigm developed by Roelfsema et al. (1998) (Fig. 1A). On each trial, the monkey was presented with two curved lines, only one of which was connected via a small segment to the fixation point [Khayat et al., 2006, their Fig. 1a (<http://www.jneurosci.org/cgi/content/full/26/1/138/FIG1>)]. The monkey's task was to maintain its gaze on the fixation point for 800 ms and then saccade to the end of the target curve, the line connected to the fixation point. Roelfsema et al. (1998) have shown previously that neurons in V1 respond more strongly to such task-relevant curves, compared with distractor curves (i.e., curves that are task-irrelevant because they are not connected to the fixation point) [see also Khayat et al., 2006, their Fig. 2a–d (<http://www.jneurosci.org/cgi/content/full/26/1/138/FIG2>)]. This selective modulation has been interpreted as a neuronal correlate of visual attention being directed to the target curve.

Khayat et al. (2006) extended the curve-tracking task to investigate the dynamics of attention. In addition to the “normal trials” described above, they introduced “switch trials,” in which the monkey had to shift attention during the course of a trial (Fig. 1B), because the connection to the fixation point was changed while the monkey was waiting to saccade. Hence, the distractor curve became a target, and vice versa, thus changing the destination of the upcoming sac-

cade [Khayat et al., 2006, their Fig. 1b (<http://www.jneurosci.org/cgi/content/full/26/1/138/FIG1>)]. The authors report that activity of neurons in area V1 reflects this change of behavioral relevance on a rapid time scale [Khayat et al., 2006, their Fig. 2e–g (<http://www.jneurosci.org/cgi/content/full/26/1/138/FIG2>)]. Remarkably, enhancement of responses caused by shifting attention to the new target curve occurred ~60 ms earlier than suppression of responses caused by removal of attention from the new distractor [Khayat et al., 2006, their Fig. 3 (<http://www.jneurosci.org/cgi/content/full/26/1/138/FIG3>)]. The 60 ms transition period, in which attention is already allocated to a new object before it is disengaged from a previously attended one, is incompatible with serial models of attentional shifts in which attention first has to be disengaged from an object before it can be shifted and allocated to another object (Shulman et al., 1979). Although Khayat et al. (2006) provide conclusive evidence against such serial models, further experiments are needed to test other models of attention that might account for the observed temporal pattern, such as split foci (McMains and Somers, 2004) or widening of the attentional focus (Müller et al., 2003).

To allow a direct comparison of neural responses during switch and normal trials the putative signal to switch attention had to occur at a fixed time (400 ms in this case) after the trial begin, making the onset of the switch signal predictable. Hence, after 400 ms, the animals were left without doubt about the task demands in the on-

Received Feb. 1, 2006; accepted Feb. 17, 2006.

Correspondence should be addressed to Laura Busse, German Primate Center, Cognitive Neuroscience Laboratory, Kellnerweg 4, 37707 Göttingen, Germany. E-mail: lbusse@gwdg.de.

DOI:10.1523/JNEUROSCI.0459-06.2006

Copyright © 2006 Society for Neuroscience 0270-6474/06/263885-02\$15.00/0

going trial (“switch” or “stay focused”). Primates have a precise internal representation of trial timing (Janssen and Shadlen, 2005), and the data of Khayat et al. (2006) suggest that their animals made use of it. In particular, responses during normal trials, in which no switch occurred, seem to decrease strongly after ~550 ms [Khayat et al., 2006, their Fig. 3*a*, dotted lines (<http://www.jneurosci.org/cgi/content/full/26/1/138/FIG3>)], suggesting that the monkeys’ level of attention dropped after they had acquired some certainty that they were performing a normal trial. Because the authors compute the latency of attentional modulation using the difference of activity between switch and normal trials, the anticipation of the switch time might affect their estimates of absolute latencies. However, these absolute latencies do not alter their main finding, namely the relative temporal relationship between attentional enhancement and suppression.

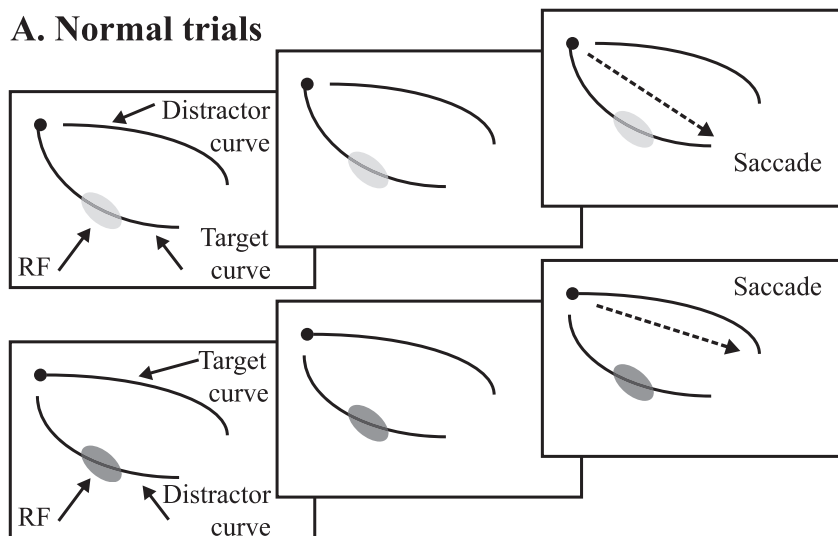
It is remarkable that the size of the attentional enhancement after shifting attention to the new target curve seems to exceed the effect of short-term adaptation during normal trials [Khayat et al., 2006, their Fig. 3*a*, red solid line vs black dotted line (<http://www.jneurosci.org/cgi/content/full/26/1/138/FIG3>)]. However, because activity drops during normal trials, the extra attentional benefit for new targets is difficult to interpret. Here, it will be interesting to investigate, in further experiments, whether this additional enhancement also holds true in designs avoiding temporal predictability. This, in turn, would raise intriguing questions about the interaction between short-term adaptation and attention.

In summary, Khayat et al. (2006) provide the first detailed analyses of the temporal dynamics of attentional modulation during shifts of attention in visual area V1. Their data convincingly demonstrate that shifts of attention cannot simply be attributed to serial subprocesses that are executed sequentially but that attention can be allocated quickly to a new object even before it is disengaged from the previously attended one.

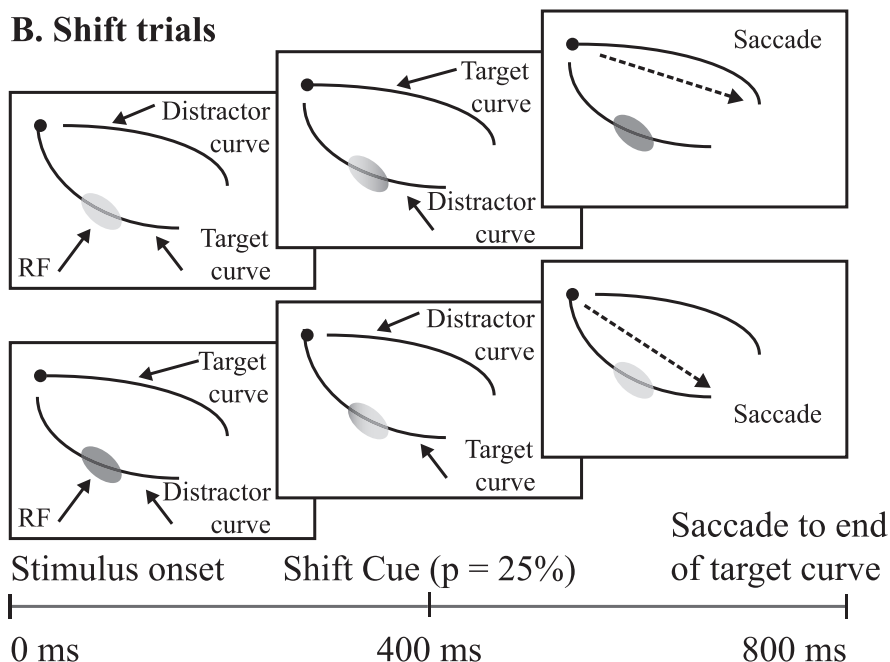
## References

Janssen P, Shadlen M (2005) A representation of the hazard rate of elapsed time in macaque area LIP. *Nat Neurosci* 8:234–241.

## A. Normal trials



## B. Shift trials



**Figure 1.** Curve-tracing task in normal (**A**) and shift trials (**B**). The shaded ellipse illustrates a V1 receptive field (RF). **A**, During normal trials, the monkey fixates on a fixation point (black circle) for 800 ms before making a saccade to the end of the line connected to the fixation point (target curve). Roelfsema et al. (1998) have demonstrated an increase in V1 activity if the curve segment inside the RF belongs to the target versus distractor curve (indicated by light gray and dark gray shading, respectively). **B**, During shift trials, the small line segment connecting the target curve to the fixation point is switched, thereby interchanging target and distractor curves. Khayat et al. (2006) show that this change of behavioral relevance is reflected in the activity of V1 neurons, leading to a fast and strong enhancement, only later followed by suppression (indicated by the gradients in the shading).

Khayat PS, Spekreijse H, Roelfsema PR (2006) Attention lights up new object representations before the old ones fade away. *J Neurosci* 26:138–142.

McMains SA, Somers DC (2004) Multiple spotlights of attentional selection in human visual cortex. *Neuron* 42:677–686.

Müller NG, Bartelt OA, Donner TH, Villringer A, Brandt SA (2003) A physiological correlate

of the “Zoom Lens” of visual attention. *J Neurosci* 23:3561–3565.

Roelfsema PR, Lamme VA, Spekreijse H (1998) Object-based attention in the primary visual cortex of the macaque monkey. *Nature* 395:376–381.

Shulman GL, Remington RW, McLean JP (1979) Moving attention through visual space. *J Exp Psychol Hum Percept Perform* 5:522–526.