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## Envisioning the Reward

**The primary visual cortex (area V1) is for vision. At least, that is what most researchers believe. However, in a recent issue of *Science*, Shuler and Bear demonstrate a correlate of reward timing in area V1. This surprising result indicates that brain circuits for reward processing are more extensive than expected and that area V1 has more functionality than previously thought.**

How do animals learn to associate an appropriate behavioral response with a particular stimulus? They can learn by trying out various responses and by monitoring the ensuing rewards and punishments (e.g., Pearce and Hall, 1980). All that is needed in this form of learning (instrumental conditioning) is that correct responses are followed by a reward, while incorrect responses are not. Animals are also capable of learning the correct response when rewards are delivered after a delay. In this case, the animal should learn not only the association between the stimulus, the response, and the reward, but also when to expect the reward (Sutton and Barto, 1998; Schultz and Dickinson, 2000).

Neuronal activity related to reward delivery and reward timing has been observed in several brain regions, including the substantia nigra and the ventral tegmental area (Schultz and Dickinson, 2000), striatum (Morris et al., 2004), amygdala (Paton et al., 2006), parietal cor-

tex (Glimcher, 2004), and frontal cortex (Tremblay and Schultz, 2000). Reward coding has so far not been observed in early sensory areas like the primary visual cortex (e.g., in monkeys; P.R.R., unpublished data). This situation has now been changed by a recent report by Shuler and Bear (2006) in *Science*, who demonstrate that activity related to reward delivery and reward timing can occur at the earliest stages of visual information processing. They found that, when adult rats experienced a pairing between a visual stimulus and a subsequent reward, a substantial fraction of neurons in the primary visual cortex began to express activity that predicted the timing of the reward.

In Shuler and Bear's experiment, rats had to lick a water tube in response to a visual stimulus to obtain a reward in the form of a drop of water (Figure 1A). The visual stimulus was presented via head-mounted goggles, which delivered large-field retinal illumination for 0.4 s to either the right or the left eye whenever the rats came near a water tube. The drop of water was given after a delay that was different for right and left eye stimulation. After stimulation of the left eye, the rat had to lick the water tube a few times (six or ten licks) to receive the reward, whereas after stimulation of the right eye it had to lick twice as many times. During the task, the activity of neurons in the primary visual cortex was monitored with chronically implanted arrays of microelectrodes.

In animals inexperienced with the task, V1 responses were found to be directly related to the physical aspects of the stimulus, such as onset, offset, and duration of the retinal illumination. Thus, in this phase, the neurons behaved just like ordinary neurons in an early visual area. However, once the animals had become proficient in the task (after three to seven training sessions), a significant proportion of neurons began to show activity that correlated with the time that the reward was given. Figure 1C shows a neuron with a poststimulus response that peaks at reward time. The response was not a result of the delivery of reward itself, because on unrewarded trials (Figure 1C, top right) the neuron showed the same response as on rewarded trials. Other neurons were found that signaled reward time by a sustained increase or a sustained decrease in their response until the reward was expected.

Another remarkable finding was that poststimulus activity related to reward timing was triggered in any given neuron by stimulation of either the left or the right eye (but not both). For the neuron shown in Figure 1C, for example, reward timing activity only occurred in response to stimulation of the left eye, and not in response to stimulation of the right eye (Figure 1C, bottom two panels). This excludes the possibility that the neuronal activity is a direct reflection of the animal's arousal, which would be similar for left and right eye stimulation. Moreover, the reward timing activity continued to be evoked by the same visual stimuli when the animals were not performing the task—that is, in sessions where access to the water tube was obstructed.

How are neurons in the primary visual cortex informed about the timing of rewards? Shuler and Bear do not speculate on this, but one possibility would be through feedback connections. Not only does the primary visual cortex project to higher cortical areas, but it also receives extensive feedback connections from these

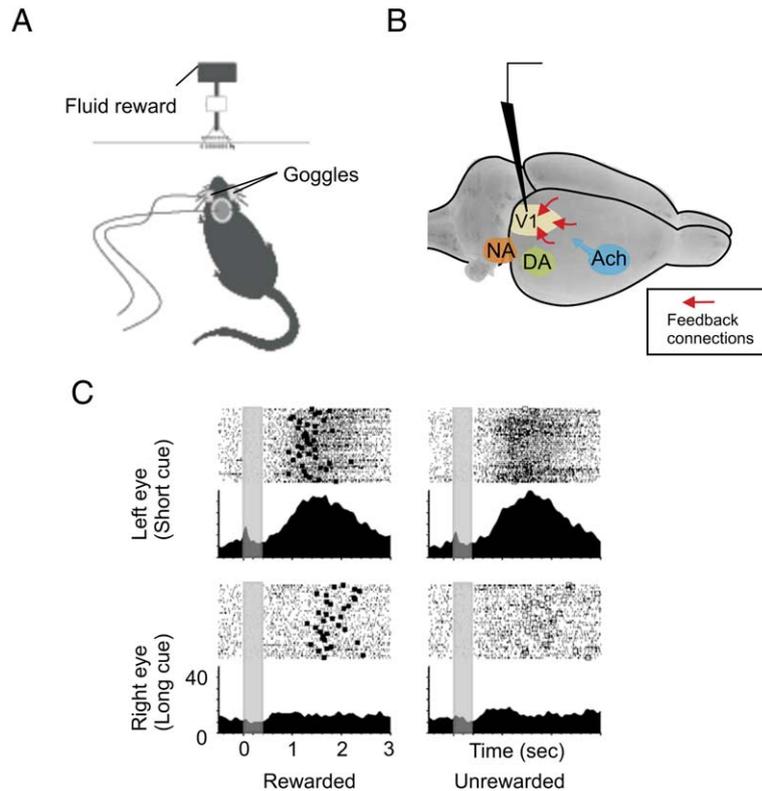


Figure 1. Reward Coding in the Primary Visual Cortex

(A) Rats had to lick a metal tube to receive a liquid reward. Visual stimuli were presented through head-mounted goggles while neurons were recorded from the primary visual cortex.

(B) Reward timing information could reach the primary visual cortex by feedback connections from higher areas (red arrows), or through neuromodulatory systems that release acetylcholine (ACh), noradrenaline (NA), or dopamine (DA).

(C) V1 neuron with a response peaking at the time of reward delivery. The gray band indicates the time of visual stimulation. Filled squares on raster plots indicate the time of reward delivery. (Upper panels) The neuron only responded to a stimulus in the left eye, indicating that the rat had to lick for a few times to get reward. (Lower panels) The neurons did not respond after right eye stimulation. The neuronal response did not depend on whether the reward was actually delivered (left panels) or not (right panels). From Shuler and Bear (2006).

areas (red arrows in Figure 1B). Feedback connections can propagate activity from areas involved in reward processing (Schultz and Dickinson, 2000; Glimcher, 2004; Paton et al., 2006) and motor programming back to the sensory cortex (Moore and Armstrong, 2003). An alternative route for reward information to reach area V1 is through neuromodulators, such as acetylcholine, dopamine, and noradrenaline. Schultz and coworkers have convincingly demonstrated that dopamine is released following stimuli that predict rewards (e.g., Ljungberg et al., 1993; Schultz and Dickinson, 2000). However, dopamine innervation to the primary visual cortex is relatively sparse, and other modulators may also be involved (Pennartz, 1995). Finally, reward information could reach V1 indirectly through changes in the animal's behavior associated with receiving or anticipating a reward. A change in eye position, for example, is known to influence activity in area V1 (Trotter and Celebrini, 1999). We note, however, that this rather trivial explanation is less likely for two reasons. First, the rats kept licking on the water tube after reward delivery, while the activity of the neurons returned back to baseline (Figure 1C). Second, the reward timing activity was also observed when the stimuli were presented outside the task.

What could be the function of reward signals in area V1? One possibility is that they could influence synaptic plasticity to improve visual perception. By using appropriate reward schedules, animals can be trained to perform difficult visual discrimination tasks. In such cases, V1 neurons increase their sensitivity to the diagnostic features of the stimuli, i.e., those features by which the stimuli can be distinguished. Also, in human subjects, plasticity in early visual areas is important for improve-

ments in challenging perceptual tasks (Hochstein and Ahissar, 2002; Schwartz et al., 2002). Neural network studies indicate how synaptic plasticity in early visual areas can maximize the neuronal sensitivity to diagnostic features, if plasticity is influenced not only by pre- and postsynaptic activity but also by reward signals (Roelfsema and van Ooyen, 2005). However, in these models it is not essential that the activity of V1 neurons themselves encodes reward delivery.

Future studies will have to unravel the advantages of reward coding in early sensory areas. Moreover, it is important to know whether the present findings extend to other sensory areas and other species. Such studies will undoubtedly advance our understanding of how rewards are predicted, how they change the neuronal circuitry, and why they are represented at both higher and lower levels of the neuronal processing hierarchy.

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