It was nice not seeing you: perceptual learning about rewards in the absence of awareness

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Abstract

In this issue of Neuron, Seitz et al. show that humans exhibit enhanced perceptual discrimination for visual stimuli that have been repeatedly paired with reward under conditions of suppressed awareness. These findings challenge the view that awareness and focused attention are necessary for perceptual learning.

KEYWORDS: perceptual learning; reward learning; awareness; attention;

Humans and other animals must constantly survey their environment to detect subtle changes that may have behaviorally significant consequences. Stimuli signaling important events, such as warning about the imminence of a predator or indicating the availability of a food source, become privileged in their neural processing, compared to other less prescient stimuli. There are at least two aspects to this phenomenon. First, stimuli associated with rewarding or punishing consequences through learning come to initiate non-volitional behavioral responses. For example, a stimulus predicting food might elicit salivation, orienting and approach behavior, commonly termed Pavlovian conditioned responses. Secondly, the sensory processing of such stimuli becomes enriched, enabling enhanced recognition and superior discrimination of these relative to other similar yet non behaviorally-relevant stimuli, a form of perceptual learning. Much is now known about the putative neural mechanisms underlying both of these aspects of conditioning. While the amygdala, orbitofrontal cortex and dopaminergic midbrain among other regions are known to contribute to the associative aspects of Pavlovian conditioning (O'Doherty, 2004), such learning in the perceptual domain depends, in part, on changes in plasticity which modifies neural representations of relevant stimuli in sensory cortex (Weinberger, 1995). A key issue for understanding both of these kinds of learning concerns the role that attention plays. Increasing the attention paid to stimuli likely leads to improvements in learning about the associations involving such stimuli (Pearce and Bouton, 2001), but also necessarily contributes to the enhancement of the perceptual processing of such stimuli (Posner and Petersen, 1990). Yet, whether attention and its more esoteric cousin "awareness" are required for learning to occur is a subject of considerable debate in the literature (Lovibond and Shanks, 2002; Wiens and Ohman, 2002).

Seitz et al., in this issue of Neuron, address whether awareness is necessary for the perceptual aspects of learning during conditioning. In a series of behavioral experiments, food and water deprived human volunteers were exposed to multiple presentations of sinusoidal gratings featuring two distinct orientations. In the first experiment one of these orientations was paired with the subsequent delivery of a small quantity of water, an appetitive stimulus for the thirsty subjects, thereby presumably faciliating the formation of a Pavlovian appetitive association between the stimulus grating and the reward. After multiple days of training with the stimuli and rewards, subjects were asked to detect each of these two orientations under noisy conditions. Compared to a pre-training baseline measure, subjects showed significantly improved perceptual discrimination for the orientation paired with reward compared to the unrewarded orientation, as would be expected given the well established phenomenon of discrimination learning during conditioning, described above. The allocation of increased attention to the rewarded orientation during the learning period, and its concomitant "awareness" may have contributed to improved perceptual discrimination.

However, the key manipulation lies in their subsequent experiment. Here, a different group of subjects underwent a similar procedure in which two grating orientations were repeatedly presented, one of which was paired with reward. On this occasion however, the gratings were presented monocularly while a series of bright contour rich patterns were rapidly flashed to the other eye. This procedure has been dubbed "continuous flash suppression" (CFS; Tsuchiya and Koch, 2005) and has the interesting property that the rapidly flashing stimuli dominates subjective awareness, banishing from awareness the stimuli presented to the alternate eye. Thus by using CFS, the authors attempted to render the grating stimuli unconscious and, by virtue of being outside of awareness, arguably beyond the reach of attention. Remarkably, after the training epoch a subsequent discrimination test revealed that subjects still showed significantly enhanced perceptual discrimination for the orientation that had been paired with reward compared to the one that had not. Yet a recognition test consisting of a presentation of the same CFS procedure and the grating stimuli to separate eyes indicated that subjects were not better than chance at reporting the presence of either stimulus, suggesting that these stimuli were indeed beyond awareness.

These findings add to our understanding of awareness in conditioning, showing that not only can unconsiously presented stimuli elicit conditioned responses, as has been shown previously (Ohman & Mineka, 2001), but that sensory perceptual representations of these stimuli can be modulated without entering awareness. Moreover, while unconscious learning during aversive conditioning is oft-studied, the role of awareness in reward conditioning has received very little focus (for an exception, see Pessiglione et al., 2008).

The current findings also expose new and interesting questions. Predominantly, this behavioral study invites a neural examination of the elements involved in unconscious reward learning. For example, where does the neural plasticity occur which enables the observed unconscious perceptual learning? The cortex would appear to represent the most likely site but the fact that learning was largely specific to the trained eye suggests that the changes occur very early on in the sensory pathways, before visual information from both eyes converges. Moreover, are the neural changes present during unconscious perceptual learning qualitatively different from those involved during learning under conditions of awareness? A prosaic possibility is that learning under these two conditions might exert similar neural effects differing according to the magnitude of the changes in the perceptual strength of the stimuli. Another question is by what neural mechanisms are the plasticity changes underlying such learning accomplished. The neuromodulator dopamine has been characterised as playing a key role in learning about rewards (Schultz, Dayan, and Montague, 1997) but dopamine is not known to have strong projections to sensory cortical areas, so is perhaps unlikely to have involvement in the sensory aspects of learning during conditioning. On the other hand the neurotransmitter acetylcholine is thought to be involved in sensory learning (Weinberger, 1995), although it is also suggested to contribute to the control of attention (Yu & Dayan, 2005).

On a cautionary note there are some who contend that learning without awareness has not been convincingly demonstrated (Lovibond & Shanks, 2002) by challenging the extent to which behavioral assays have succeeded in verifying that subjects are truly unaware of stimulus contingencies. A conciliatory position might be that conscious and unconscious learning is better viewed not as a dichomoty but rather a continuum along which stimuli vary in the extent that they activate sensory representations. Regardless, it is clear that studies such as the present which probe the boundaries of human learning will help to provide new behavioral tools for the study of the neural mechanisms underlying reward, learning, attention and their interactions.

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