2. Helbing, D., Molnar, P., Farkas, I.J., and Bolday, K. (2001). Self-organizing pedestrian movement. Environment and Planning B: Planning and Design *28*, 361–383.
3. Parrish, J.K., and Edelstein-Keshet, L. (1999). Complexity, pattern, and evolutionary trade-offs in animal aggregation. Science *284*, 99–101.
4. Schneirla, T.C. (1944). A unique case of circular milling in ants, considered in relation to trail following and the general problem of orientation. American Museum Novitates *1253*, 1–26.
5. Buhl, J., Sumpter, D.J., Couzin, I.D., Hale, J.J., Despland, E., Miller, E.R., and Simpson, S.J. (2006). From disorder to order in marching locusts. Science *312*, 1402–1406.
6. Parrish, J.K., Viscido, S.V., and Grunbaum, D. (2002). Self-organized fish schools: an examination of emergent properties. Biol. Bull. *202*, 296–305.
7. Angelini, T.E., Hannezo, E., Trepat, X., Marquez, M., Fredberg, J.J., and Weitz, D.A. (2011). Glass-like dynamics of collective cell migration. Proc. Natl. Acad. Sci. USA *108*, 4714–4719.
8. Zhang, H.P., Be'er, A., Florin, E.L., and Swinney, H.L. (2010). Collective motion and density fluctuations in bacterial colonies. Proc. Natl. Acad. Sci. USA *107*, 13626–13630.
9. Szabo, B., Szollosi, G.J., Gonci, B., Juranyi, Z., Selmeczi, D., and Vicsek, T. (2006). Phase transition in the collective migration of tissue cells: experiment and model. Phys. Rev. E Stat. Nonlin. Soft Matter Phys. *74*, 061908.
10. Liu, L., Tuzel, E., and Ross, J.L. (2011). Loop formation of microtubules during gliding at high density. J. Phys. Condens. Matter *23*, 374104.
11. Schaller, V., Weber, C., Semmrich, C., Frey, E., and Bausch, A.R. (2010). Polar patterns of driven filaments. Nature *467*, 73–77.
12. Lindemann, C.B., and Lesich, K.A. (2010). Flagellar and ciliary beating: the proven and the possible. J. Cell Sci. *123*, 519–528.
13. Dixit, R., and Cyr, R. (2004). Encounters between dynamic cortical microtubules promote ordering of the cortical array through angle-dependent modifications of microtubule behavior. Plant Cell *16*, 3274–3284.
14. Peterman, E.J., and Scholey, J.M. (2009). Mitotic microtubule crosslinkers: insights from mechanistic studies. Curr. Biol. *19*, R1089–R1094.

Department of Bioengineering, 229 Hallowell Building, Pennsylvania State University, University Park, PA 16802, USA.
E-mail: wohbio@engr.psu.edu

DOI: 10.1016/j.cub.2012.04.045

Associative Learning: Pavlovian Conditioning without Awareness

Can Pavlovian conditioning occur outside of awareness? Yes, according to a new study showing that, under a particular set of circumstances, visual stimuli can become associated with aversive outcomes without participants ever seeing the stimuli.

Joel Pearson

There is an ongoing debate as to the role of conscious awareness in Pavlovian conditioning. This process, in which neural representations of events correlated in the world become linked in the neural systems representing them, is often measured behaviourally by distinct physiological reflexes. Associative learning became famously linked to the work of Ivan Pavlov and his experiments on salivation in dogs. Pavlov's work involved ringing a bell right before the dogs were fed. He learnt that with time the dogs would actually salivate in response to the sound of the bell alone, showing they had learned the association between the bell and the food.

Despite forms of conditioning having been demonstrated in a diverse range of organisms including the sea slug *Aplysia* [1], the question as to the role of awareness in this process of learning has stirred up considerable debate [2]. Studying conscious awareness in non-human animals that cannot explicitly report their phenomenological experience often comes with thorny philosophical assumptions about interpreting behaviour, so most work on the role of awareness has involved human participants. Until recently, much of this research has been hindered by methodological constraints. A paper in this issue of *Current Biology* by Raio *et al.* [3] reports perhaps the most compelling evidence to date that Pavlovian conditioning can arise without conscious awareness.

The authors utilised a relatively new technique developed for studying vision and visual awareness called 'continuous flash suppression' [4–6]. Continuous flash suppression is more or less a form of binocular rivalry pushed to its extreme. During binocular rivalry two dissimilar visual patterns are presented, one to each eye, so the observer's brain is forced to try and reconcile these two very different images to exist at the one place simultaneously. Rather than seeing one transparent fused coherent stable image, observers see something often initially shocking — their visual awareness of the two patterns alternates back and forth over time, in no predictable manner. While each pattern is presented to and processed by one eye and subsequent brain areas, an individual sees only one of the patterns, while the other is suppressed outside of awareness. This process provides a valuable opportunity to examine the extent of neural processing and effects of visual stimuli on behaviour without awareness. Forms of binocular rivalry have been utilised to study many processes and phenomena outside of awareness, such as spatial orientation processing [7], motion perception [8], emotion [9], object processing [10] and even sexual orientation [11].

Continuous flash suppression has similar properties to binocular rivalry, but one of the images continuously flickers (at ~10 Hz) between different brightly coloured patterns. These bright flashes (or coloured visual transients) have the power to supress a stimulus in the other eye for extended periods, often for a few seconds. Continuous flash suppression is thus one of the most powerful methods for rendering a normal visual stimulus invisible.

Raio *et al.* [3] used continuous flash suppression to render images of male and female faces invisible or outside of awareness. For half of these invisible presentations one set of faces, say the males, was immediately followed by a brief electrical shock to the wrist, while the female set was not. Randomly interleaved between these reinforced trials were non-reinforced test-trials of both male and female faces (still visually suppressed). The skin conductance response during these test-trials increased after only a few presentations of the training or conditioning trials. In other words, the associative learning effect (greater skin conductance to the faces that were followed by a shock) occurred even though the subjects were never aware of the face stimuli during the conditioning or test trials. Furthermore, the authors had participants report if they saw a face on each trial; in fact participants had to make a two-alternative forced-choice decision whether the face was male or female — participants' decisions were just below chance. After this discrimination task participants had to rate the confidence of their choice — confidence ratings were no higher on correct trials than incorrect trials.

The conditioning or learning effects outside of awareness reported by Raio *et al.* [3] display some distinct characteristics that differentiate them from learning with awareness. The learning effects appeared very rapidly and subsequently diminished very rapidly. Unlike normal learning these effects faded during further conditioning, whereas typically in this kind of conditioning experiment the learning would continue before stabilising. Such brevity in associative learning dynamics is clearly distinct from typical conditioning effects, which often last for days. Might this learning outside of awareness be tapping into a categorically different learning mechanism, or perhaps a subset of normal learning processes? This is an interesting idea that is compatible with the data in the new study [3].

Raio *et al.* [3] did include a fully visible condition, which showed a very different temporal learning profile. In their visible condition, however, both the learning and test-trials were both visible, while in the unaware condition both the training and test-trials were invisible. Hence, we do not have a conscious measure of conditioning outside of awareness, only an unconscious one. To help clarify the underlying mechanism what is needed is a third condition in which only the test trials are visible while the training trials remain suppressed from awareness. Such an experiment would help tease apart the nature of this unconscious learning.

Previous claims of unconscious conditioning have been criticised on a number of methodological grounds such as trial sequence artifacts, failure to assess participant hypotheses, and insensitivity to partial awareness [2]. In fact, some researchers have gone so far as to argue that all conditioning involves cognitive representation and hence conscious awareness [12]. Others maintain that conditioning is carried out by a separately evolved specialised system [13,14]. Will continuous flash suppression finally provide the experimental tool to resolve this long-standing debate? Watch this space!

Associative learning is thought to form the backbone of the mechanisms of many psychological disorders and their treatments [15,16]. Many behavioural interventions for psychological disorders rely on counterconditioning or extinction-like approaches, such as cognitive behavioural therapy. Does this new paper by Raio *et al.* [3] shed light on any new clinical treatment possibilities? Potentially yes, if mechanisms of associative learning can operate without awareness, it is possible to imagine a future non-intrusive treatment option that might be run on patients without their conscious involvement. However, the brief lifetime of the effects in the new paper might limit any potential clinical applications.

References

1. Carew, T.J., Walters, E.T., and Kandel, E.R. (1981). Classical conditioning in a simple withdrawal reflex in Aplysia californica. J. Neurosci. *1*, 1426–1437.
2. Lovibond, P.F., and Shanks, D.R. (2002). The role of awareness in Pavlovian conditioning: empirical evidence and theoretical implications. J. Exp. Psychol. Anim. Behav. Proc. *28*, 3–26.
3. Raio, C., Carmel, D., Carrasco, M., and Phelps, E.A. (2012). Nonconscious fear is quickly acquired but swiftly forgotten. Curr. Biol. *22*, R477–R479.
4. Tsuchiya, N., and Koch, C. (2005). Continuous flash suppression reduces negative afterimages. Nat. Neurosci. *8*, 1096–1101.
5. Tsuchiya, N., Koch, C., Gilroy, L.A., and Blake, R. (2006). Depth of interocular suppression associated with continuous flash suppression, flash suppression, and binocular rivalry. J. Vis.n *6*, 1068–1078.
6. Stein, T., Hebart, M.N., and Sterzer, P. (2011). Breaking continuous flash suppression: a new measure of Uunconscious processing during interocular suppression? Front. Hum. Neurosci. *5*, 167.
7. Pearson, J., and Clifford, C.W. (2005). Suppressed patterns alter vision during binocular rivalry. Curr. Biol. *15*, 2142–2148.
8. Blake, R., Tadin, D., Sobel, K.V., Raissian, T.A., and Chong, S.C. (2006). Strength of early visual adaptation depends on visual awareness. Proc. Natl. Acad. Sci. USA *103*, 4783–4788.
9. Pasley, B.N., Mayes, L.C., and Schultz, R.T. (2004). Subcortical discrimination of unperceived objects during binocular rivalry. Neuron *42*, 163–172.
10. Almeida, J., Mahon, B.Z., Nakayama, K., and Caramazza, A. (2008). Unconscious processing dissociates along categorical lines. Proc. Natl. Acad. Sci. USA *105*, 15214–15218.
11. Jiang, Y., Costello, P., Fang, F., Huang, M., and He, S. (2006). A gender- and sexual orientation-dependent spatial attentional effect of invisible images. Proc. Natl. Acad. Sci. USA *103*, 17048–17052.
12. Mitchell, C.J., De Houwer, J., and Lovibond, P.F. (2009). The propositional nature of human associative learning. Behav. Brain Sci. *32*, 183–198, discussion 198–246.
13. Clark, R.E., and Squire, L.R. (1998). Classical conditioning and brain systems: the role of awareness. Science *280*, 77–81.
14. Ohman, A., and Mineka, S. (2001). Fears, phobias, and preparedness: toward an evolved module of fear and fear learning. Psychol. Rev. *108*, 483–522.
15. Rauch, S.L., Shin, L.M., and Phelps, E.A. (2006). Neurocircuitry models of posttraumatic stress disorder and extinction: human neuroimaging research–past, present, and future. Biol. Psych. *60*, 376–382.
16. Milad, M.R., Rauch, S.L., Pitman, R.K., and Quirk, G.J. (2006). Fear extinction in rats: implications for human brain imaging and anxiety disorders. Biol. Psychol. *73*, 61–71.

School of Psychology, The University of New South Wales, Sydney, Australia.
E-mail: Joel@pearsonlab.org

DOI: 10.1016/j.cub.2012.04.042

Nuclear Positioning: Dynein Needed for Microtubule Shrinkage-Coupled Movement

Nuclear movement often requires interactions between the cell cortex and microtubules. A new study has revealed a novel protein interaction linking microtubule plus-ends with the cortex and a role for dynein in microtubule shrinkage-coupled movement.

Xin Xiang

Proper positioning of nuclei and mitotic spindles is crucial for the normal growth and development of many eukaryotic organisms [1]. Unlike other cellular organelles that move along microtubule tracks, nuclei/spindles move in response to either pushing or pulling force on the microtubules