neuroimaging results should be used with appropriate caution. There is, at present, no validated objective 'consciousness meter' that can be used as proof or disproof of awareness in severely brain-damaged patients. As pointed out by Owen *et al.* [17], a more powerful approach to identify 'volition without action' in patients who are unable to communicate their experiences might be to scan patients while they are asked to perform a mental imagery task, rather than using the passive external stimulation paradigms described above. Reproducible and anatomically specific activation in individual patients during tasks that unequivocally require 'willed action' or intentionality for their completion could be argued to reflect awareness unambiguously. Of course, *negative* findings in the same circumstances could not (and should not) be used as evidence for lack of awareness.

At present, much more data and methodological validation is urgently needed before functional neuroimaging studies can be proposed to the medical community as a tool to disentangle the clinical 'gray zone' that separates vegetative states from states of minimal consciousness.

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Letters

# Illusory motion reversal in tune with motion detectors

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Occasionally during prolonged viewing, a continuously illuminated moving pattern seems to reverse direction [1]. Kline *et al.* suggested that this illusory motion reversal (IMR) could originate in spurious responses of classical Reichardt motion detectors[2]; however, others consider the phenomenon to be an analogue of the wagon wheel illusion and take it as evidence that the visual system processes the world using discrete samples [1,3–5]. In their recent article supporting the discrete sampling theory, Andrews and Purves [3] highlight a recent finding that IMR occurs most often for stimuli with a particular temporal frequency rather than a particular velocity. In other words, IMR appears to be temporal-frequency tuned. According to Andrews and Purves, this contradicts the theory that the illusion results from spurious responses of Reichardt motion detectors because, they claim, 'Reichardt motion detectors are tuned to velocity rather than temporal frequency' (p.263).

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This last claim, a crucial one for their argument, is erroneous. Only the delay-and-correlate subcomponent of the Reichardt motion unit is velocity-tuned [6]. Full Reichardt detectors, which compute the difference between subcomponents preferring opposite directions of motion, are temporal-frequency tuned [7]. Furthermore, although the subcomponents are indeed tuned to the velocity of a pattern moving in the correct direction, they do not show velocity tuning when responding to a pattern moving in the wrong direction. To see why, imagine that the delay-and-correlate subcomponent is presented with a moving periodic pattern of dots (as in Figure 1A of [2]). First, a dot stimulates the delayed input line of the correlator. Next, although the pattern moves in the 'non-preferred' direction, a second, trailing dot stimulates the undelayed input line at exactly the time necessary to activate the correlator. If the spatial frequency of this hypothetical dot pattern were lowered, the stimulus velocity would have to be increased in order to continue stimulating the detector. This demonstrates that the correlator's activity is not velocity-tuned for motion in the 'non-preferred' direction.

A separate discrete sampling process is therefore not necessary to explain the IMR. The 10–15 Hz tuning of the illusion [4] coincides with the overall frequency tuning of normal human motion sensitivity [8]. This is compatible with the Kline *et al.* theory of rivalry between oppositely-tuned motion detectors [2]. Prolonged stimulation would lead to extreme adaptation of motion units, especially when that stimulation is presented at the temporal frequency for which the system is most sensitive. In turn, this could occasionally allow relatively unadapted detectors selective for the reverse direction to drive the percept.

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Letters Response

# The wheels keep turning

***Reply to Holcombe et al.***

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In their original paper, Kline *et al.* [1] explained the wagon-wheel illusion in continuous light (WWIc) [2] in terms of Reichardt motion detectors [3]. We initially questioned this conclusion because such detectors are primarily tuned to velocity rather than temporal frequency [4], whereas the preferred temporal behavior of the WWIc remains constant over a range of spatial frequencies [5,6]. The authors now counter that their case rested on a subcomponent of Reichardt detectors that *is* velocity tuned, but only in the forward direction, and that the full detector is in fact sensitive to temporal frequency [7]. Thus, they argue, aliasing of such detectors remains a viable explanation.

It is indeed possible that a subset of detectors with appropriate spatio-temporal parameters could induce competition within a population of motion detectors, and that such rivalry might generate epochs of veridical motion and reversed motion [1]. There are, however, important weaknesses in this line of argument. First, there is no evidence that Reichardt detectors exist in the mammalian visual system. Second, this sort of mechanism would have to explain why the illusion occurs at a similar temporal frequency for both first- and second-order motion [5], which is difficult to explain given that the optimal temporal sensitivity to first- and second-order motion is markedly different [8]. Finally, it is not clear how Reichardt detectors could account for the dependence of the WWIc on attention [5]. What is clear from this exchange is that physiological evidence rather than further speculation will be needed to establish why a stimulus moving in one direction is periodically perceived

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