Journal Club

Editor's Note: These short, critical reviews of recent papers in the *Journal*, written exclusively by graduate students or postdoctoral fellows, are intended to summarize the important findings of the paper and provide additional insight and commentary. For more information on the format and purpose of the Journal Club, please see http://www.jneurosci.org/misc/ifa_features.shtml.

Propagating Cortical Waves May Underlie Illusory Motion Perception

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Review of Rekauszke et al.

Motion-inducing illusions can reveal basic mechanisms of motion processing by separating the contributions of local versus global mechanisms within the motion detection hierarchy. In studies of animals (Conway et al., 2005; Tuthill et al., 2011) and humans (Seghier and Vuilleumier, 2006), stimuli that induce illusory motion have activation patterns consistent with corresponding real motion in the visual pathway (Clifford and Ibbotson, 2002; Mascalzoni and Regolin, 2011). Numerous theoretical models propose motion detection circuits that carry out computational comparisons of light varying across space and time (Borst and Euler, 2011), but exploring such circuits in cortex is a considerable methodological challenge. In a recent publication in the *Journal of Neuroscience*, Rekauszke et al. (2016) described how temporal asymmetries in On and Off streams of visual processing affect activation dynamics in primary visual cortex (V1).

Visual information is divided into parallel streams in the retina that respond either

to increments (On pathway) or decrements (Off pathway) of illumination, with the Off pathway having a faster temporal response (for review, see Euler et al., 2014). These temporal asymmetries in the latency of the parallel pathways persist through the retina and visual thalamus and into V1 (Jin et al., 2011). Rekauszke et al. (2016) hypothesized that these asynchronies in On and Off latencies generate motion signals in V1. Such signals may be the underlying mechanism of illusory motion percepts elicited by a myriad of stimuli, such as the line motion illusion (Steinman et al., 1995) and the peripheral drift illusion (Faubert and Herbert, 1999), which is shown in Figure 1.

Rekauszke et al. (2016) used voltage-sensitive dyes (VSDs) and extracellular electrodes to measure neuronal activity in anesthetized cat visual cortex and to test whether the temporal asymmetries in On and Off processing produce motion signals. A visual stimulus consisting of spatially separated high- and low-luminance squares underwent simultaneous counterchanges of luminance, generating propagating waves of activity in V1. The direction of propagation was consistent with the reported perception of motion in human subjects. These waves accelerated in the direction of illusory motion, and the response magnitude was subadditive, suggesting that nonlinear interactions between the stimulus locations may mediate wave properties. When the luminance change was the same for both locations, the wave propagation was symmetric,

suggesting that the temporal asymmetry between On and Off pathways was the source of the motion signal.

Overall, the experiment by Rekauszke et al. (2016) was well designed. The results of the VSD approach—an ideal technique for studying large-scale dynamics in cortex—were validated using electrophysiology. Stimuli parameters were suitable for probing temporal dynamics in visual processing; and were controlled for stimuli adaptation, unequal offset latencies, and background illumination (thereby dissociating contrast differences and luminance differences). The authors also demonstrated that when stimuli were the same at each location, the waves were symmetric. These critical controls strongly suggest that temporal differences between On and Off were the source of asymmetric propagation, favoring the conclusion that cortical waves encode motion information.

However, there are a few methodological issues that could influence the interpretation of the results. The stimuli were generated by a CRT monitor at 100 Hz, so each stimulus was displayed for 10 ms. If there were any visible phosphor persistence during the stimulus transition, there could have been temporal offsets in the stimuli themselves (Jonides et al., 1982; Irwin et al., 1983). Also, differences between metered and perceived luminance may have led to bright and dark stimuli being of unequal perceptual contrast relative to background (Baker, 1963; Di Lollo et al., 1997). Propor-

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Figure 1. Peripheral drift illusion. Sawtooth luminance wheels viewed in the periphery generate an illusory motion percept during rapid blinking or by generating an afterimage. The motion is perceived from dark to bright such that the above stimuli are seen as rotating inward toward fixation (center dot). Based on the study by Rekauszke et al. (2016), one might predict that each eye blink generates a wave across visual cortex that propagates along the gradient from dark to bright. The figure was modified from Faubert and Herbert (1999).

tional increments and decrements in luminance are not perceptually symmetric and could potentially explain why human participants always perceived the bright stimulus as being in motion (Lu and Sperling, 2012). A separate methodological consideration is that the physiology experiments were conducted under anesthesia, which could produce different neuromodulator activity and altered cortical state compared with alert animals (Silver et al., 2008; Harris and Thiele, 2011).

There are also conceptual considerations that could have strengthened the experimental results. One interesting observation was that the response magnitude elicited by the joint luminance counterchange of the two stimuli was subadditive when compared with the expected magnitude from each stimulus in isolation. Mechanisms such as surround suppression that reduce the response to a pair of stimuli independent of any temporal asymmetries or motion signals (Albright and Stoner, 2002) may account for this result. An approach that would remove the confound between the number of stimuli and the motion content of the stimuli would be to compare the response magnitude of two bright stimuli turning dark with the response magnitude of the counterchange of one dark and one bright stimulus. The authors performed this experiment to demonstrate that the wave does not propagate asymmetrically when the spatially separated stimuli have the same luminance (Rekauszke et al., 2016, their Fig. 4), but they did not compare the summation of these two stimulus conditions to show that the subadditive quality is special for the motion-inducing condition.

Another consideration that could have strengthened the results concerns the controls the authors performed. One control was to vary the permutations of background illumination to show that the evoked traveling waves were independent of the back-

ground condition. A second control was to show that the motion component is absent if the stimuli are of the same sign. While these experiments show that the wave propagation is likely caused by On and Off temporal asymmetries, it appears that the human subjects did not participate in these control conditions. Stimulus conditions that failed to elicit asymmetric waves in cortex should also fail to elicit illusory motion percepts. Without this validation it remains unclear whether the two phenomena are perfectly correlated.

There are many exciting follow-up experiments to explore beyond the results of Rekauszke et al. (2016). If waves propagating across V1 are a cause of motion perception, then one would predict a relationship between the perceived speed of motion and the speed of the wave propagation. Previous work on cortical waves has found them to decelerate as they approach adjacent cortical areas and reflect back at the boundary (Xu et al., 2007). Are there perceptual motion signals that match these wave properties? What parameters break the illusion and what is the effect on cortical waves? One could test wave dynamics across space and time by sampling many stimulus locations (including luminance counterchanges across the vertical meridian) and by using various stimulus-onset asynchronies such that On leads or lags Off.

An additional question is whether the asymmetric spread of activation is due to feedforward inputs inherited from the retina, recurrent connections in V1, or feedback from other cortical areas. The temporal asynchrony may be generated by On and Off inputs from LGN, as suggested by Rekauszke et al. (2016). Alternatively, MT, a motion-processing center that also receives direct input from LGN, may generate motion signals from the visual input and feed those signals back into V1 through the large reciprocal tracts connecting these two visual areas. Targeting V1 and MT in follow-up experiments could help to identify where the motion signals originate. Inactivation of MT or V1 could also help to test whether these areas are necessary for the presence of waves.

A final dimension to explore in the relationship between propagating waves and motion processing in cortex is contrast. Previous theoretical accounts (Sato et al., 2012) have proposed the reduction of spatial integration under high-contrast conditions, compared with low-contrast conditions. Others have shown the properties of traveling waves in cortex to be contrast dependent (Nauhaus et al., 2009), with low-contrast stimuli evoking larger waves and high-

contrast stimuli evoking smaller waves. However, Rekauszke et al. (2016) conducted experimental manipulations only under high contrast. Normalization models of cortical activity would predict the increased expansion of the traveling wave in low-contrast conditions compared with high-contrast conditions (Carandini and Heeger, 2012). Low-contrast stimulation might drive less suppression in the spread of the wave activation, while high-contrast stimulation would limit wave dynamics because of stronger suppression (Sit et al., 2009; Sato et al., 2012). Would this contrast-dependent change in wave dynamics result in a corresponding change in the perception of illusory motion?

In conclusion, Rekauszke et al. (2016) provide a cortical explanation for apparent motion illusions elicited by contrast reversals. They also provide a possible role for propagating cortical waves in the encoding of motion information. Previous experiments have characterized both spontaneously occurring and visually evoked traveling waves (Nauhaus et al., 2009, 2012), and one previously proposed mechanism of motion processing in V1 is the dynamic temporal interactions between feedforward and horizontal connections (Seriès et al., 2002). Are propagating waves a ubiquitous property of visual stimulation, or are they specific to stimulation that is temporally offset? If propagating waves occur independently of any perception of illusory motion, do they have other perceptual consequences? Whether these motion signals are an artifact of the temporal differences between On and Off visual pathways or a feature in the functional hierarchy of the motion detection circuitry used to extract information based on changes in illumination in the visual scene remains to be explored.

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