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.

The Relationship between Visual Awareness, Attention, and Report

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Review of Wyart and Tallon-Baudry (http://www.jneurosci.org/cgi/content/full/28/10/2667)

Attention and awareness seem to be intimately related. Intuitively, it seems logical that we become aware of events that we attend to, whereas information outside the scope of our attention remains undetected. Indeed, some have argued that there is a tight relationship between attention and awareness (Posner, 1994; O'Regan and Noe, 2001), whereas others have claimed that attention and awareness are different (Lamme, 2003). Although attention and awareness are difficult to disentangle in practice, in a recent paper in The Journal of Neuroscience, Wyart and Tallon-Baudry (2008) elegantly demonstrated that distinct neural processes might be involved in both functions.

Wyart and Tallon-Baudry (2008) recorded magnetoencephalographic signals while human subjects performed a task in which faint gratings were presented at an attended or unattended location (on some trials no stimulus was presented). After each trial, participants indicated which of two orientations they thought matched the previously presented grating and whether they had seen the grating. Trials were classified as aware (grating was detected and orientation was identified correctly) or as unaware (grating was not de-

tected and orientation was identified at chance level). Spatial attention increased the likelihood of conscious report: more gratings were consciously seen at the attended location (\sim 50%) than at the unattended location (\sim 40%). Additionally, attention shortened reaction times on the orientation discrimination task for consciously seen gratings, but not for unseen gratings. Thus, visual awareness and attention seemed to interact at the behavioral level.

Comparing oscillatory brain activity between seen and unseen trials as well as between attended and unattended trials enabled the authors to determine the neural responses related to visual awareness and spatial attention, respectively. The authors specifically focused on gammaband oscillation, which has been suggested to reflect recurrent synchronization and as such has been implicated in both visual awareness and spatial attention. The awareness-related contrast revealed a significant increase in midfrequency gamma-band activity (54-64 Hz) 240-500 ms after grating presentation. Crucially, this awareness-related effect did not differ between attended and unattended trials. Conversely, attended versus nonattended stimuli caused a significant increase in high-frequency gamma-band activity (76–90 Hz) slightly later in time (350-500 ms) and was uniquely modulated by attention (and not by conscious experience). Although partially overlapping, the effects turned out to be topographically specific, both peaking contralateral to stimulus presentation at occipital and occipitoparietal sensors. Moreover, single-subject correlational analyses showed that awareness- and attention-related activity was unrelated on a trial-by-trial basis.

Together, these results suggest that attention and awareness operate independently at a neural level. As predicted, the awareness-related gamma activity correlated highly with the probability of conscious report across subjects, but, interestingly, the attention-related gamma-band modulation did also, albeit to a smaller degree. Thus, although neural processes of attention and awareness seem to be independent with respect to location, timing, and gamma-band frequency, they both correlate with conscious report.

From the data, the authors conclude that awareness and attention interact at the behavioral level, but not at the neural level. The authors suggest a solution for this apparent contradiction by postulating that visual awareness and attention contribute independently to a third category of neural activity: "a perceptual threshold about the presence (or absence)" of a stimulus. Although this is not made explicit, such a solution implies that there is more than one type of "perception"; one related to visual awareness per se (the awareness-related gamma activity), and one related to the conscious re-

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D01:10.1523/JNEUROSCI.1208-08.2008 Copyright © 2008 Society for Neuroscience 0270-6474/08/285401-02\$15.00/0 port of a stimulus (their detection measure which correlates with both their attention- and awareness-related activity).

Indeed, some have proposed the existence of two types of awareness: "phenomenal" awareness and "access" awareness (Lamme, 2003; Block, 2005). Phenomenal awareness represents the raw neural representation of perceptual (visual) information, which is represented in the occipital cortex; access awareness reflects the ability to report about this representation. In such a scheme, attentional selection may operate to boost information transfer to access awareness, such that phenomenal awareness and attention may operate completely independently, although activity changes in either may influence what is reported.

Wyart and Tallon-Baudry's (2008) finding that awareness- and attention-related activity operated independently although both correlated with conscious report fits nicely with this proposed dichotomy in visual awareness. The finding that awareness-related activity preceded attention-related activity further strengthens this conclusion. But why did they not find their suggested third category of neural activity? And what might a correlate of access awareness look like?

Based on much evidence, several researchers have suggested that large-scale interactions between high-level executive areas and low-level perceptual areas are necessary for transferring information to a reportable stage (Rees et al., 2002; Lamme, 2003; Dehaene et al., 2006). For example, a previous EEG study by Melloni et al. (2007) showed that conscious report was selectively correlated with increased frequency-coupling of gamma-band activity (50-57 Hz) across occipital, parietal, and frontal electrodes. Such results suggest that access awareness may be associated with increased phase coupling between anterior and posterior brain areas, but not with an increase in gamma-band power by itself. Assessing frequency coupling in the study by Wyart and Tallon-Baudry (2008) could potentially uncover this relationship and could easily be achieved by running additional analyses. The prediction would be that increased phase coupling correlates best with report and shows strong correlations with both attention- and awareness-related activity, as does the behavioral measure.

Another important issue relates to the question of what a "perceptual threshold" actually is. Evidence suggests that conscious report is the outcome of a decision process that sits between sensory analysis and final motor output (Super et al., 2001). For instance, a previous functional magnetic resonance imaging study by Lau and Passingham (2006) showed that within-subject differences in subjective report under equal levels of objective performance are associated with different levels of activity in the mid-dorsolateral prefrontal cortex. Such studies suggest that subjective report is influenced by criterion setting, and that the "perceptual threshold" that Wyart and Tallon-Baudry (2008) suggest is not an absolute threshold, but a relative one. The importance of a decision-related process in visual awareness is illustrated by their finding that false alarms (a report of the presence of a stimulus when none was presented) were associated with increased midfrequency awareness-related activity and correlated with report. Apparently, the overall difficulty of the task and the criterion that subjects set themselves allowed some spontaneous midfrequency activity to be interpreted as evidence of signal presence. But because their awareness measure was composed of both an objective forcedchoice decision about stimulus orientation and a subjective yes/no decision, it was inherently less sensitive to differences in criterion setting than if their awareness measure would have been purely subjective (yes/no only). On one hand, this is a

positive feature of their study because making their awareness measure more objective prevents unwanted uncontrollable confounds of criterion setting, but on the other hand, this does not allow gauging of the way decision processes relate to conscious report. Such gauging could have been achieved by using a paradigm that allowed the objective detection measure to be held constant while the report about subjective experience varied, like in the Lau et al. study (2006), or by systematically manipulating the decision criterion by varying the number of stimulusabsent trials, as in the study by Super et al. (2001).

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