

- 2 Vandenberg, A.R.E. *et al.* (2014) Seeing without knowing: neural signatures of perceptual inference in the absence of report. *J. Cogn. Neurosci.* 26, 955–969
- 3 Block, N. (2011) Perceptual consciousness overflows cognitive access. *Trends Cogn. Sci.* 15, 567–575
- 4 Cohen, M. and Dennett, D. (2011) Consciousness cannot be separated from function. *Trends Cogn. Sci.* 15, 358–364
- 5 Phillips, I.B. (2011) Perception and iconic memory: what Sperling doesn't show. *Mind Lang.* 26, 381–411
- 6 Bronfman, Z. *et al.* (2014) We see more than we can report: 'cost free' color phenomenality outside focal attention. *Psychol. Sci.* 25, 1394–1403
- 7 Asplund, C. *et al.* (2014) The attentional blink reveals the probabilistic nature of discrete conscious perception. *Psychol. Sci.* 25, 824–831
- 8 Ling, S. *et al.* (2009) How spatial and feature-based attention affect the gain and tuning of population responses. *Vision Res.* 49, 1194–1204
- 9 Frässle, S. *et al.* (2014) Binocular rivalry: frontal activity relates to introspection and action but not to perception. *J. Neurosci.* 34, 1738–1747
- 10 Leopold, D. *et al.* (2002) Visual processing in the ketamine-anesthetized monkey: optokinetic and blood oxygenation level-dependent responses. *Exp. Brain Res.* 143, 359–372

Inferior frontal junction biases perception through neural synchrony

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How the primate attentional control network interacts with posterior sensory regions to bias perception is not fully understood. Using magnetoencephalography (MEG) supplemented by functional magnetic resonance imaging (fMRI), a recent study reported that human inferior frontal junction (IFJ) could play a key role in biasing perception through neural synchrony with posterior sensory regions.

Our visual world is filled with a continuous influx of visual information. The ability to attend, select, and encode what is most relevant to the task at hand is vital to everyday visual cognition. For example, when driving on a busy street, we need to attend constantly to road signs, moving cars, and pedestrians while ignoring a host of other nonessential visual inputs. Decades of cognitive neuroscience research have provided us with rich details of the neural mechanisms mediating attention and selection. In their influential review work, Corbetta and Shulman [1] outlined two parietal-frontal circuits that are involved in the control of top-down and bottom-up visual attention. Later work by Yantis and Serences [2] highlighted the role of superior parietal lobule (SPL) in initiating attentional switching between different locations, different features of the same attended object, and different input modalities. More recently, Xu and Chun [3] showed that goal-directed object representation can be achieved by distinct parietal mechanisms in a two-step process with the inferior intraparietal sulcus (IPS) selecting objects via their locations and the superior IPS encoding the detailed features of the selected objects. In recent monkey neurophysiological studies [4,5], neural synchronies among frontal, parietal, and sensory regions have been shown to play an important role in attentional modulation of sensory processing. Despite these advances, little research has examined in humans how the attentional control network interacts

with posterior sensory regions to bias perception, and whether neural synchrony plays a role in this process.

In a recent study, using MEG supplemented by fMRI to optimize both temporal and spatial resolution, Baldauf and Desimone [6] addressed this pivotal question. They presented human subjects with two streams of images, one containing a sequential presentation of faces and the other houses. The two streams were presented at slightly different temporal frequencies to allow each stream to be tagged by a unique frequency. Baldauf and Desimone overlapped the two image streams at the exact same spatial location and asked subjects to attend either the faces or the houses, and detect a one-back image repetition in the attended stream. They then used fMRI to localize two sensory regions that show preference to the processing of faces and houses, which are the fusiform face area (FFA) [7] and the parahippocampal place area (PPA) [8], respectively. Baldauf and Desimone also localized a brain region involved in non-spatial attention in the IFJ. Using these regions of interests to guide the analysis of MEG signals, they examined the power of MEG signals at the tagging frequency for faces and houses. They found that FFA was more responsive to the face tagging frequency only when faces were attended and, similarly, PPA was more responsive to the house tagging frequency only when houses were attended. Thus, sensory responses in FFA and PPA were modulated by top-down attention according to the task demand. Interestingly, the IFJ responded to the tagging frequency of the attended objects regardless of whether faces or houses were attended. In other words, IFJ was synchronized with FFA when faces were attended, and with PPA when houses were attended (Figure 1). By analyzing the phase-lags between IFJ and FFA/PPA, Baldauf and Desimone further discovered that IFJ was leading FFA/PPA with a constant time-lag of about 20 ms. The IFJ thus appeared to be the driver of the synchrony. Additional analysis with diffusion tensor imaging confirmed that IFJ is connected to both FFA and PPA, providing anatomical support for its role in biasing perception in posterior regions through neural synchrony.

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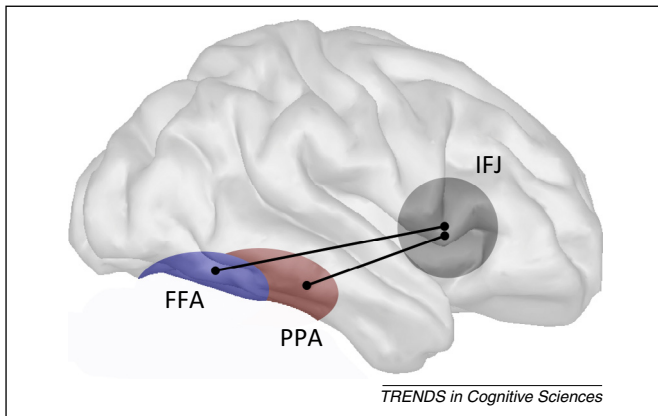


Figure 1. Interaction between the inferior frontal junction (IFJ) and the fusiform face area (FFA)/parahippocampal place area (PPA). When showing two overlapping streams of faces and houses, the human IFJ was synchronized with FFA when faces were attended, and with PPA when houses were attended. Phase-lags between IFJ and FFA/PPA revealed that IFJ was leading FFA/PPA with a constant time-lag of about 20 ms. This suggests that IFJ may be the driver of the synchrony, allowing it to be engaged flexibly in attentional selection of different objects appearing at the same spatial location. Reproduced, with permission, from [6].

Baldauf and Desimone [6] thus revealed for the first time how IFJ may participate in attention-biased perception through neural synchrony with posterior regions where the actual sensory signals are contained. These results are consistent with findings from a previous study by Asplund and colleagues [9]. By examining fMRI time courses, Asplund *et al.* found that the IFJ was either coupled with the dorsal attention system in a top-down goal-directed task, or with the ventral attention system in a bottom-up stimulus-driven attention capture task. They concluded that top-down and bottom-up attention are linked together through activities in the IFJ, allowing the brain to be engaged flexibly in either type of attentional control. The MEG neural synchrony results from Baldauf and Desimone complement those from Asplund *et al.* by showing that the IFJ can also be flexibly engaged in attentional selection of different objects appearing at the same spatial location. Together, these two studies highlight the ability of the IFJ to be coupled with different posterior mechanisms to bias perception.

These findings generate intriguing questions to be addressed in future research. For example, given the role of SPL in initiating attentional switching between different locations, different features of the same attended object, and different input modalities [2], how does IFJ

interact with SPL when attention is switched from attending to faces to attending to houses in the study of Baldauf and Desimone [6]? Is SPL the driver of IFJ? The dorsal lateral prefrontal cortex (DLPFC) has been shown to maintain task-relevant information by directing attention to internal representations of sensory stimuli and motor plans that are stored in more posterior regions [10]. How should we understand the unique roles of IFJ and DLPFC during attentional control, and how do these two brain regions interact? In addition, given that both MEG and fMRI provide correlational measures rather than causal connections between brain and behavior, it would be important for future monkey neurophysiological studies and human transcranial magnetic stimulation studies to test the causal role of IFJ in attentional control and behavior.

Nevertheless, with the combination of different neuroimaging approaches including MEG and fMRI, and measuring neural synchrony between different brain regions, the study by Baldauf and Desimone [6] opens up a whole new area of research wherein key questions regarding how attention may modulate perception in the human brain can now be addressed.

Acknowledgments

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References

- 1 Corbetta, M. and Shulman, G.L. (2002) Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* 3, 201–215
- 2 Serences, J.T. and Yantis, S. (2006) Selective visual attention and perceptual coherence. *Trends Cogn. Sci.* 10, 38–45
- 3 Xu, Y. and Chun, M.M. (2009) Selecting and perceiving multiple visual objects. *Trends Cogn. Sci.* 13, 167–174
- 4 Buschman, T.J. and Miller, E.K. (2007) Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science* 315, 1860–1862
- 5 Gregoriou *et al.* (2009) High-frequency, long-range coupling between prefrontal and visual cortex during attention. *Science* 324, 1207–1210
- 6 Baldauf, D. and Desimone, R. (2014) Neural mechanisms of object-based attention. *Science* 344, 424–427
- 7 Kanwisher, N. *et al.* (1997) The fusiform face area: a module in human extrastriate cortex specialized for the perception of faces. *J. Neurosci.* 17, 4302–4311
- 8 Epstein, R. and Kanwisher, N. (1998) A cortical representation of the local visual environment. *Nature* 392, 598–601
- 9 Asplund, C.L. *et al.* (2010) A central role for the lateral prefrontal cortex in goal-directed and stimulus-driven attention. *Nat. Neurosci.* 13, 507–512
- 10 Curtis, C.E. and D'Esposito, M. (2003) Persistent activity in the prefrontal cortex during working memory. *Trends Cogn. Sci.* 7, 415–423