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Top-Down Suppression

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Glossary

Selective attention Goal-directed focus on task-relevant information while ignoring other irrelevant information.

Top-down enhancement Targeted upregulation of neural representations of relevant information.

Top-down suppression Downregulation of neural representations of irrelevant information.

Working memory System for actively maintaining and manipulating relevant information over a short period of time.

Introduction

Amid a sea of incoming sensory stimulation, it is essential to prioritize the processing of those few pieces of information that are most relevant to one's current behavioral goals. The controlled regulation of sensory processing is known as top-down modulation, reflecting the influence that higher-order attentional control systems exert upon lower-level perceptual systems. This construct can be further broken down into two components that operate in tandem. Top-down enhancement refers to the targeted upregulation of neural representations of relevant information, whereas top-down suppression refers to the downregulation of neural representations of irrelevant information. In some cases, the neural suppression of unattended representations may be a direct consequence of the enhancement of relevant representations, due to competitive processing dynamics between neural ensembles with different spatial receptive fields or stimulus-selectivity profiles (Desimone & Duncan, 1995; Lavie, 2005; Pinsk, Doniger, & Kastner, 2004). But in other cases, top-down enhancement and suppression appear to operate as independently controlled processes (Gazzaley, Cooney, Rissman, & D'Esposito, 2005; Luck et al., 1994; Moher, Lakshmanan, Egeth, & Ewen, 2014) that may utilize distinct brain networks (Chadick & Gazzaley, 2011; Suzuki & Gottlieb, 2013).

Neuroscientific studies often make a distinction between the source and site of top-down modulation. The source can be thought of as the region(s) of the brain – often in frontoparietal cortices – that represents information about one's current attentional priorities and sends signals to lower-level perceptual areas to influence processing in accordance with these priorities (Gilbert & Li, 2013; Miller & D'Esposito, 2005; Moore, 2006). The regions that receive these modulatory signals and consequently show attention-dependent changes in their level of activity can be thought of as the sites of modulation. Although many insights into the mechanisms of attentional control have come from neurophysiological studies of nonhuman animals (reviewed in Gilbert & Li, 2013), in this article, we focus on insights that have emerged from neuroimaging studies in humans. We further limit our review to studies examining the suppression component of top-down control, with an emphasis on data from functional magnetic resonance imaging (fMRI) and electroencephalography/magnetoencephalography (EEG/MEG). Since the majority of studies on top-down suppression have used visual tasks, we will concentrate on findings from

the visual domain. We note, however, that task-irrelevant representations in any modality can be willfully suppressed, including the representations of motor action plans.

Selective Attention

Selective attention refers to the goal-directed focus on task-relevant information while ignoring other irrelevant information. Although some common mechanisms may support the selective allocation of attention in different domains, neuroimaging studies of selective attention often use tasks that require participants to regulate the processing of a particular kind of information, such as spatial locations, perceptual features, whole objects, or internally maintained representations (e.g., items held in working memory). We will now consider each of these four expressions of selective attention in turn.

Spatial Suppression

Spatial selective attention refers to the ability to prioritize the processing of information occurring at a particular location of space. In neuroimaging studies, the mechanisms of spatial attention are often studied by instructing participants to covertly attend to stimuli in one hemifield while maintaining a central fixation. This procedure capitalizes on the contralateral organization of cortical visual processing, such that the magnitude of attentional modulation can be indexed by the respective levels of activity in the contralateral (attended) and ipsilateral (ignored) hemifields. In many cases, it is of further interest to examine the modulation of activity associated with specific locations within a hemifield. This can be accomplished by exploiting the retinotopic organization of visual cortex and identifying areas that are tuned to particular angular positions and eccentricities that correspond to the locations of attended or unattended stimuli. Using this general approach, fMRI studies have identified a 'center-surround' organization in multiple visual cortical regions (Bressler, Fortenbaugh, Robertson, & Silver, 2013; Muller & Kleinschmidt, 2004; Tootell et al., 1998) such that blood oxygen level-dependent (BOLD) activity to a target location is enhanced, but BOLD activity to surrounding locations is suppressed. The magnitude of surround suppression may vary depending on the particular visual region in question and the eccentricity of the irrelevant visual stimulus. Whereas dorsal regions (e.g., area V5

and posterior parietal cortex (PPC)) exhibit greater peripheral suppression, ventral regions (areas V1–V4 and lateral occipital cortex) yield greater suppression at more central eccentricities (Bressler et al., 2013), resulting in a center-surround profile akin to a ‘Mexican hat function’ (Hopf et al., 2006). The phenomenon of surround suppression can be obtained even in the absence of a perceptual target stimulus; the covert allocation of attention to a specific spatial location is sufficient to evoke surround suppression (Silver, Ress, & Heeger, 2007). Nor does the phenomenon require the presence of any distracting stimuli in the periphery (Boehler, Tsotsos, Schoenfeld, Heinze, & Hopf, 2011). That said, surround suppression may be more pronounced when peripheral distractors are present (Heinemann, Kleinschmidt, & Müller, 2009). Furthermore, as task difficulty increases, visual cortical activity to proximal distractors is more attenuated than neural responses to distractors at more distal eccentricities (Parks, Beck, & Kramer, 2013). Similarly, the lateral geniculate nucleus (LGN) of the thalamus has been shown to decrease BOLD activity to unattended locations, and the magnitude of this suppression effect increases as task difficulty increases (O’Connor, Fukui, Pinsk, & Kastner, 2002). Such findings suggest that top-down factors may play a role in specifying the need for additional suppression at the spatial locations of potentially distracting stimuli and showcase that suppression may operate at the earliest stages of visual processing, which include the LGN (O’Connor et al., 2002), pulvinar (Strumpf et al., 2013), and V1 (Tootell et al., 1998). Indeed, neuroimaging techniques with higher temporal resolution, such as EEG and MEG, have found that surround suppression effects emerge as early as 50–150 ms post stimulus onset (Hopf et al., 2006; Slotnick, Hopfinger, Klein, & Sutter, 2002).

Whereas spatially selective regions in visual cortex are well established as sites of top-down suppression, many regions have been proposed as sources of these top-down signals (Corbetta & Shulman, 2002; Gilbert & Li, 2013). For instance, in anticipation of a potentially distracting stimulus that an observer has reason to believe will appear at a particular location, a network of frontoparietal regions are mobilized to proactively suppress processing at that location, including the frontal eye fields (Couperus & Mangun, 2010; Seiss, Driver, & Eimer, 2009), inferior frontal junction (IFJ) (Sylvester, Jack, Corbetta, & Shulman, 2008), superior frontal and angular gyri (Ruff & Driver, 2006), and precuneus (Payne & Allen, 2011). Recent progress in understanding the differential contributions of frontal and parietal structures has come from experiments in monkeys using neurophysiological recordings and reversible inactivation (Suzuki & Gottlieb, 2013). This work has confirmed that although both the lateral parietal cortex and the dorsolateral prefrontal cortex (DLPFC) help guide the selection of relevant spatial targets, neural ensembles in DLPFC play a uniquely important role in mediating the long-range inhibition of distracting visual input. The importance of DLPFC activity for visuospatial distractor suppression has also been noted in human neuroimaging work (Toepfer et al., 2010). Although we have focused on studies examining visual processing, there are data to suggest that the source of top-down spatial suppression may be modality-independent, such that irrelevant sensory cortical representations of visual, auditory, or tactile location may be attenuated by common attentional control mechanisms (Seiss, Gherri, Eardley, & Eimer, 2007).

Feature-Based Suppression

Suppressing features during selective attention usually implies ignoring elementary parts of an object, such as its color, motion, and shape. Similar to spatial suppression, the site of top-down feature suppression is typically the region(s) of the sensory cortex representing the to-be-ignored stimulus features. In the visual domain, attention to features is known to modulate neural activity in areas V1–V3, color-selective region V4, and motion-selective region V5 (Chawla, Rees, & Friston, 1999; Maunsell & Treue, 2006; Polk, Drake, Jonides, Smith, & Smith, 2008; Saenz, Buracas, & Boynton, 2002). There is some indication that the suppression of irrelevant features is associated with the modulation of neural activity during the earliest stages of visual cortical processing, as indexed by the P1 component (~100 ms post stimulus onset) of the EEG event-related potential (ERP) (Moher et al., 2014). In the case of color and motion stimuli, this early measure of attentional modulation is thought to arise in feature-selective areas V4 and V5, respectively (Schoenfeld et al., 2007). Moreover, suppression of the P1 component may be most prominent in the presence of competing stimuli, when the behavioral incentives for feature-based selection are heightened (Valdes-Sosa, Bobes, Rodriguez, & Pinilla, 1998; Zhang & Luck, 2009). Importantly, suppressing irrelevant features during the P1 component is not contingent on concurrent spatial filtering processes (Akyurek & Schubö, 2013). Indeed, feature-based attentional selection may operate throughout the visual field in a global manner, regardless of spatial attention processes (Moher et al., 2014; Saenz et al., 2002; Zhang & Luck, 2009) and even in the absence of direct visual stimulation (Serences & Boynton, 2007).

Despite some evidence for early acting effects (Moher et al., 2014), ERP markers of feature suppression in the visual cortex are not consistently observed in all people prior to 200 ms post stimulus onset (Zanto & Gazzaley, 2009; Zanto, Toy, & Gazzaley, 2010). Indeed, in one study, only individuals with superior working memory abilities suppressed the P1 (~100 ms) and N1 (~170 ms) response to irrelevant visual features (Zanto & Gazzaley, 2009). Another EEG study found that while suppression of prefrontal activity was observed ~130 ms post stimulus onset, suppression in the visual cortex was not seen until ~225 ms post stimulus onset (Daffner et al., 2012). This is in line with a previous report that feature-based suppression in the visual cortex occurs during later processing stages and may be the consequence of feature-based enhancement prior to suppression (Andersen & Müller, 2010). To reconcile conflicting reports as to when top-down feature suppression operates, two mechanisms have been proposed based on task set (Moher et al., 2014). One mechanism enables rapid enhancement of relevant features, followed by suppression of irrelevant features, when the target feature changes frequently over time. The other mechanism can suppress early visual processes when task-relevant stimuli remain consistent over time. Importantly, both mechanisms permit attentional modulation (i.e., attend > ignore) of early visual processes, one through enhancement and one through suppression. Whereas additional research will be required to address this theory, it supports the suggestion that feature-based suppression may act to both proactively prevent the allocation of attention to irrelevant features and reactively terminate attentional allocation (Sawaki, Geng, & Luck, 2012) in

circumstances where it has been involuntarily captured by salient distractors (Sawaki & Luck, 2013).

The source of feature-based attentional modulation arises from a frontoparietal network akin to that mobilized during spatial attention, suggesting that these two forms of attention may rely on a unified top-down control system (Corbetta & Shulman, 2002; Egner et al., 2008; Maunsell & Treue, 2006). Although spatial attention and feature-based attention elicit BOLD activity in overlapping frontoparietal regions, subregions of this network are thought to underlie specialized spatial or feature-based components (Giesbrecht, Woldorff, Song, & Mangun, 2003; Slagter et al., 2007). These specialized subdivisions of attentional control are prominent in the PPC (Schenkluhn, Ruff, Heinen, & Chambers, 2008) and may be represented by spatially distributed and intermixed populations of PPC neurons (Greenberg, Esterman, Wilson, Serences, & Yantis, 2010). However, it is unclear whether these subregions are uniquely specialized for suppressing, and not enhancing, neural responses to features. There is considerable evidence from lesion studies to indicate that the prefrontal cortex (PFC) is involved in top-down feature suppression, just as in spatial suppression, which operates on the sensory cortex across modalities (e.g., vision, auditory, and somatosensory) (reviewed in Knight, Staines, Swick, and Chao (1999)). However, it should be noted that PFC lesions also affect top-down enhancement abilities, which may reflect the diffuse nature of lesions rather than a reflection of overlapping control regions.

Compared to studying the consequences of naturally occurring brain lesions, research approaches that aim to temporarily perturb brain activity in healthy adults offer a more focal approach to assess top-down mechanisms. For instance, the application of transcranial magnetic stimulation (TMS) to the IFJ (which includes the posterior DLPFC) resulted in increased P1 activity in the visual cortex to irrelevant visual features and decreased P1 activity to relevant features (Zanto, Rubens, Thangavel, & Gazzaley, 2011), suggesting that enhancement and suppression may arise from the same source or from closely neighboring subregions. In the parietal cortex, TMS to the intraparietal sulcus (IPS) has been reported to selectively disrupt the ability to suppress visual cortical activity in response to distraction (Mevorach, Hodson, Allen, Shalev, & Humphreys, 2010), whereas TMS to IPS during spatial attention disrupted the enhancement of visual activity (Capotosto, Babiloni, Romani, & Corbetta, 2009). Thus, the role of IPS may differ for spatial and feature-based attention. Alternatively, differences in the exact site of IPS stimulation could have affected dissociable subregions mediating top-down enhancement and suppression. In support of a functional dissociation, enhancement and suppression of visual features have been observed to arise in overlapping parietal network regions that operate in distinct alpha band (8–12 Hz) frequencies (Bridwell & Srinivasan, 2012).

Object-Based Suppression

Visual objects are perceptual entities composed of multiple featural elements, such as color, shape, and texture, that can be identified based on the structured relationship between these features. It has been proposed that the act of selecting a

particular feature of an object to attend to results in the automatic selection of the object as a whole, including task-irrelevant features (O'Craven, Downing, & Kanwisher, 1999; Sohn, Papathomas, Blaser, & Vidnyanszky, 2004). However, using a negative priming task, it has been shown that object discrimination performance declines when a constituent feature of the object (i.e., color or motion) was previously ignored (Nobre, Rao, & Chelazzi, 2006). This suggests that the attentional control processes that mediate the suppression of irrelevant features may operate in a manner that is at least partially independent from object-level selection mechanisms.

Similar to spatial and feature-based attention, object-based attention can modulate activity throughout the visual cortex (i.e., V1–V5) (Ernst, Boynton, & Jazayeri, 2013; Pratte, Ling, Swisher, & Tong, 2013). Not surprisingly, object-based attention results in particularly strong modulatory effects in higher-level visual regions known to contribute to object recognition, such as the lateral occipital complex (Kourtzi & Kanwisher, 2001), the fusiform face area (Kanwisher, McDermott, & Chun, 1997), and the parahippocampal place area (PPA) (Epstein & Kanwisher, 1998). Notably, the latter two structures exhibit suppressed BOLD activity when young adult participants are instructed to ignore face and scene stimuli, respectively (Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005). Older adults, in contrast, show a complete failure to appropriately suppress activity in these regions, despite a preserved ability to enhance activity in these regions for relevant stimuli (Gazzaley, Cooney, Rissman et al., 2005). Using EEG to evaluate the temporal dynamics of these modulatory effects, neural suppression of irrelevant face or scene stimuli was observed as early as the P1 in younger adults, but not in older adults (Clapp, Rubens, & Gazzaley, 2010; Gazzaley et al., 2008). This selective suppression deficit occurred even when older adults were explicitly provided with prior knowledge of which upcoming stimuli would be relevant and irrelevant (Zanto, Hennigan, Ostberg, Clapp, & Gazzaley, 2010). Taken together, these findings suggest that object-based suppression mechanisms may be dissociable from object-based enhancement mechanisms, with only the former being impaired by cognitive aging. However, it is unclear if older adults' difficulty with suppression can be attributed to a problem with inhibitory control per se or whether it could be explained by diminished cognitive resources available to maintain and act upon one's current attentional priorities, resulting in the overprocessing of irrelevant information when it is initially encountered (Rissman, Gazzaley, & D'Esposito, 2009).

The source of object-based top-down modulation is generally thought to arise from the same general frontoparietal network that supports spatial and feature-based attention (Corbetta & Shulman, 2002). Although the DLPFC is consistently observed to be involved in object-based selective attention processes in the context of distraction (Postle, 2005), there is conflicting evidence as to its functional role. Some research suggests that the DLPFC serves to enhance task-relevant object representations but does not contribute to the suppression of distractors (Egner & Hirsch, 2005; Feredoes, Heinen, Weiskopf, Ruff, & Driver, 2011), while other studies have shown the DLPFC may suppress neural activity to irrelevant objects and not enhance activity to task-relevant targets (Minamoto, Osaka, & Osaka, 2010; Zanto, Chadick, Satriis, & Gazzaley, 2013). Thus, it is possible that distinct subregions exist within

DLPFC that serve to enhance or suppress distant sensory representations. Some fMRI data in support of this possibility used a functional connectivity analysis with the left PPA as a 'seed' region to identify two nearby, yet distinct, foci in the left DLPFC (~2 cm apart) that were associated with scene enhancement and scene suppression, respectively (Gazzaley et al., 2007).

In addition to DLPFC involvement in top-down object suppression, the ventrolateral PFC (VLPFC) is also known to facilitate the resolution of competition between simultaneously active representations (Badre & Wagner, 2007; Jha, Fabian, & Aguirre, 2004; Nelson, Reuter-Lorenz, Persson, Sylvester, & Jonides, 2009). For example, the VLPFC suppresses the negative impact of distractors on long-term memory performance (Wais, Kim, & Gazzaley, 2012) through functional interactions between the VLPFC, hippocampus, and visual cortex (Wais, Rubens, Boccanfuso, & Gazzaley, 2010). Of note, a high working memory load results in increased distractor processing concomitant with increased BOLD activity in the DLPFC, VLPFC, and visual cortex (de Fockert, Rees, Frith, & Lavie, 2001), highlighting the role of the DLPFC and VLPFC in resolving attentional conflict between relevant and irrelevant objects and suggesting that top-down suppression may be subject to central capacity limitations (Rissman et al., 2009).

Internally Directed Suppression

Internally oriented attention refers to the act of focusing on representations that are not present in the sensory environment. Examples include attending to information that has been retrieved from long-term memory, refreshed from working memory, generated via mental imagery, or produced

during mind wandering (i.e., undirected thinking). Not only will refreshing a working memory trace enhance BOLD activity in category-selective visual cortex such as the PPA, but also simultaneous suppression occurs in at least some category-selective cortical regions that are not refreshed (Johnson & Johnson, 2009). There are data to suggest that the frontoparietal sources of memory suppression signals for internal representations might be similar to those observed during external stimulus suppression. Specifically, increased BOLD activity in the DLPFC and PPC has been observed during tasks in which participants are explicitly instructed to block the retrieval of a given memory or to forget something that has already been learned (Anderson et al., 2004; Bastin et al., 2012; Benoit & Anderson, 2012; Gagnepain, Henson, & Anderson, 2014; Hanslmayr et al., 2012; Paz-Alonso, Bunge, Anderson, & Gheiti, 2013). These frontoparietal structures in turn act to suppress hippocampal activity and sensory/perceptual representations, ultimately resulting in increased forgetting.

Other data, however, suggest that the top-down control mechanisms for regulating attention to stimuli in the external environment may be distinct from those involved in searching one's memory and attending to the contents that are retrieved (Ciaramelli, Grady, Levine, Ween, & Moscovitch, 2010; Sestieri, Shu, & Corbetta, 2010). Indeed, these externally and internally oriented attentional control systems may even compete, such that engagement of one system transiently suppresses the other (Huijbers, Pennartz, Cabeza, & Daselaar, 2009; Sestieri et al., 2010). That said, there are data to indicate that some executive control regions such as the DLPFC (Christoff, Gordon, Smallwood, Smith, & Schooler, 2009) and IPS (Cabeza et al., 2011) are actively engaged during both external stimulus processing and introspective mentation. An important direction for future

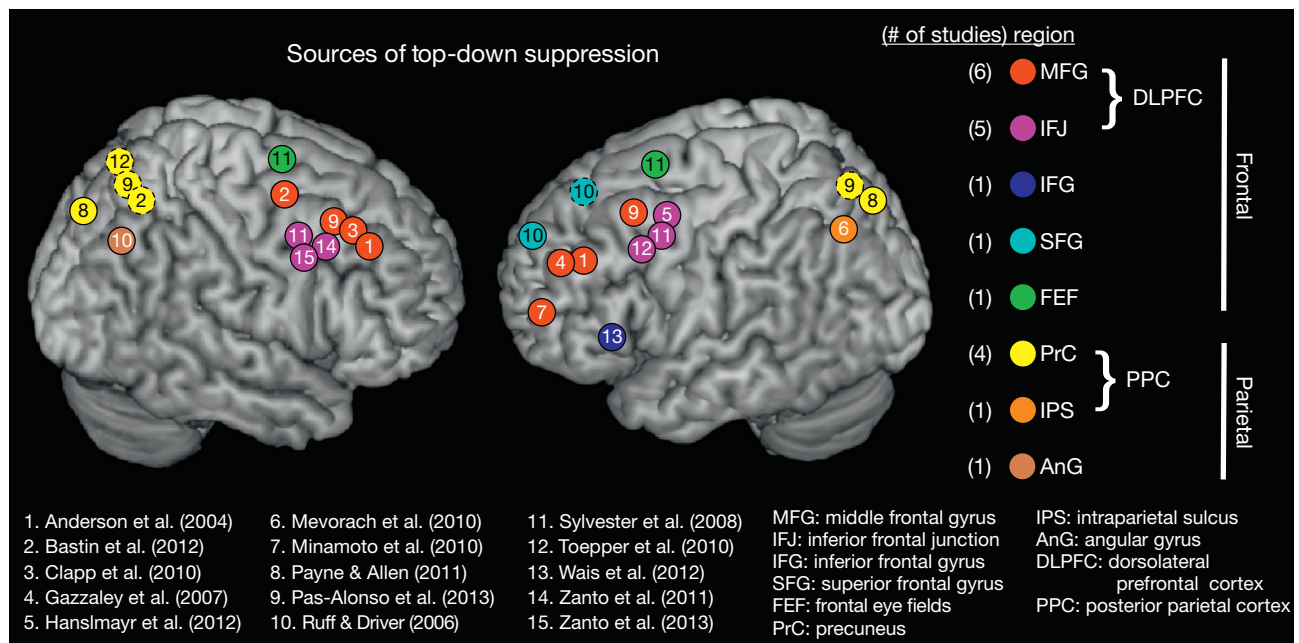


Figure 1 Sources of top-down suppression. Colored circles estimate locations of reported fMRI and/or TMS effects that are associated with suppression of neural activity in the sensory cortex. Colors of the circles represent the neural region, the number inside each circle represents the referenced article, and a dashed line around some circles indicates that the reported activity was medial to the cortical surface and has been projected outward for display purposes. The numbers in parentheses (left of the color legend) reflect the number of studies (out of the 15 reported) that identified that neural region as a source of top-down suppression.

research will be to better characterize the control processes that support the dynamic toggling of top-down suppression of the internal and external world, achieving the appropriate balance between these seemingly opposing cortical networks (Spreng, Sepulcre, Turner, Stevens, & Schacter, 2013).

Summary

Top-down suppression mechanisms operate on sensory cortices and serve to downregulate neural activity to unimportant information. The frontoparietal sources of these modulatory signals appear to be largely consistent across different types of to-be-ignored information, such as spatial locations, features, objects, or internal representations (Figure 1). Top-down suppression effects act rapidly and influence multiple stages of perceptual processing, including activity in the early visual cortex. Moreover, these effects often emerge in anticipation of a forthcoming stimulus, thereby enabling efficient suppression of neural activity to irrelevant items, reducing competition, and optimizing the pursuit of one's goals.

See also: **INTRODUCTION TO ACQUISITION METHODS:** Basic Principles of Electroencephalography; Basic Principles of Magnetoencephalography; Obtaining Quantitative Information from fMRI; **INTRODUCTION TO COGNITIVE NEUROSCIENCE:** Response Inhibition; Saliency/Bottom-Up Attention; Short-Term Memory; Working Memory; Working Memory–Attention Interplay; **INTRODUCTION TO SOCIAL COGNITIVE NEUROSCIENCE:** Mindfulness: Mechanism and Application; **INTRODUCTION TO SYSTEMS:** Face Perception; Motion Perception; Neural Codes for Shape Perception; Primate Color Vision; Visuospatial Attention; Working Memory.

References

- Akyurek, E. G., & Schubo, A. (2013). Electrophysiological correlates of early attentional feature selection and distractor filtering. *Biological Psychology, 93*, 269–278.
- Andersen, S. K., & Muller, M. M. (2010). Behavioral performance follows the time course of neural facilitation and suppression during cued shifts of feature-selective attention. *Proceedings of the National Academy of Sciences of the United States of America, 107*, 13878–13882.
- Anderson, M. C., Ochsner, K. N., Kuhl, B., Cooper, J., Robertson, E., Gabrieli, S. W., et al. (2004). Neural systems underlying the suppression of unwanted memories. *Science, 303*, 232–235.
- Badre, D., & Wagner, A. D. (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. *Neuropsychologia, 45*, 2883–2901.
- Bastin, C., Feyers, D., Majerus, S., Baiteau, E., Degueldre, C., Luxen, A., et al. (2012). The neural substrates of memory suppression: A fMRI exploration of directed forgetting. *PLoS One, 7*, E29905.
- Benoit, R. G., & Anderson, M. C. (2012). Opposing mechanisms support the voluntary forgetting of unwanted memories. *Neuron, 76*, 450–460.
- Boehler, C. N., Tsotsos, J. K., Schoenfeld, M. A., Heinze, H. J., & Hopf, J. M. (2011). Neural mechanisms of surround attenuation and distractor competition in visual search. *The Journal of Neuroscience, 31*, 5213–5224.
- Bressler, D. W., Fortenbaugh, F. C., Robertson, L. C., & Silver, M. A. (2013). Visual spatial attention enhances the amplitude of positive and negative fMRI responses to visual stimulation in an eccentricity-dependent manner. *Vision Research, 85*, 104–112.
- Bridwell, D. A., & Srinivasan, R. (2012). Distinct attention networks for feature enhancement and suppression in vision. *Psychological Science, 23*, 1151–1158.
- Cabeza, R., Mazuz, Y. S., Stokes, J., Kragel, J. E., Woldorff, M. G., Ciaramelli, E., et al. (2011). Overlapping parietal activity in memory and perception: Evidence for the attention to memory model. *Journal of Cognitive Neuroscience, 23*, 3209–3217.
- Capotosto, P., Babiloni, C., Romani, G. L., & Corbetta, M. (2009). Frontoparietal cortex controls spatial attention through modulation of anticipatory alpha rhythms. *The Journal of Neuroscience, 29*, 5863–5872.
- Chadick, J. Z., & Gazzaley, A. (2011). Differential coupling of visual cortical areas with the default network or frontal-parietal network based on task goals. *Nature Neuroscience, 14*, 830–832.
- Chawla, D., Rees, G., & Friston, K. J. (1999). The physiological basis of attentional modulation in extrastriate visual areas. *Nature Neuroscience, 2*, 671–676.
- Christoff, K., Gordon, A. M., Smallwood, J., Smith, R., & Schooler, J. W. (2009). Experience sampling during fMRI reveals default network and executive system contributions to mind wandering. *Proceedings of the National Academy of Sciences of the United States of America, 106*, 8719–8724.
- Ciaramelli, E., Grady, C., Levine, B., Ween, J., & Moscovitch, M. (2010). Top-down and bottom-up attention to memory are dissociated in posterior parietal cortex: Neuroimaging and neuropsychological evidence. *The Journal of Neuroscience, 30*, 4943–4956.
- Clapp, W. C., Rees, G., & Gazzaley, A. (2010). Mechanisms of working memory disruption by external interference. *Cerebral Cortex, 20*, 859–872.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews. Neuroscience, 3*, 201–215.
- Couperus, J. W., & Mangun, G. R. (2010). Signal enhancement and suppression during visual-spatial selective attention. *Brain Research, 1359*, 155–177.
- Daffner, K. R., Zhuravleva, T. Y., Sun, X., Tarbi, E. C., Haring, A. E., Rentz, D. M., et al. (2012). Does modulation of selective attention to features reflect enhancement or suppression of neural activity? *Biological Psychology, 89*, 398–407.
- de Fockert, J. W., Rees, G., Frith, C. D., & Lavie, N. (2001). The role of working memory in visual selective attention. *Science, 291*, 1803–1806.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience, 18*, 193–222.
- Egner, T., & Hirsch, J. (2005). Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. *Nature Neuroscience, 8*, 1784–1790.
- Egner, T., Monti, J. M. P., Trittschuh, E. H., Wieneke, C. A., Hirsch, J., & Mesulam, M. M. (2008). Neural integration of top-down spatial and feature-based information in visual search. *The Journal of Neuroscience, 28*, 6141–6151.
- Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature, 392*, 598–601.
- Ernst, Z. R., Boynton, G. M., & Jazayeri, M. (2013). The spread of attention across features of a surface. *Journal of Neurophysiology, 110*, 2426–2439.
- Feredoes, E., Heinen, K., Weiskopf, N., Ruff, C., & Driver, J. (2011). Causal evidence for frontal involvement in memory target maintenance by posterior brain areas during distracter interference of visual working memory. *Proceedings of the National Academy of Sciences of the United States of America, 108*, 17510–17515.
- Gagnepain, P., Henson, R. N., & Anderson, M. C. (2014). Suppressing unwanted memories reduces their unconscious influence via targeted cortical inhibition. *Proceedings of the National Academy of Sciences of the United States of America, 111*, E1310–E1319.
- Gazzaley, A., Clapp, W., Kelley, J., McEvoy, K., Knight, R., & D'Esposito, M. (2008). Age-related top-down suppression deficit in the early stages of cortical visual memory processing. *Proceedings of the National Academy of Sciences of the United States of America, 105*, 13122–13126.
- Gazzaley, A., Cooney, J. W., McEvoy, K., Knight, R. T., & D'Esposito, M. (2005). Top-down enhancement and suppression of the magnitude and speed of neural activity. *Journal of Cognitive Neuroscience, 17*, 507–517.
- Gazzaley, A., Cooney, J. W., Rissman, J., & D'Esposito, M. (2005). Top-down suppression deficit underlies working memory impairment in normal aging. *Nature Neuroscience, 8*, 1298–1300.
- Gazzaley, A., Rissman, J., Cooney, J., Rutman, A., Seibert, T., Clapp, W., et al. (2007). Functional interactions between prefrontal and visual association cortex contribute to top-down modulation of visual processing. *Cerebral Cortex, 17*, 1125–1135.
- Giesbrecht, B., Woldorff, M. G., Song, A. W., & Mangun, G. R. (2003). Neural mechanisms of top-down control during spatial and feature attention. *NeuroImage, 19*, 496–512.
- Gilbert, C. D., & Li, W. (2013). Top-down influences on visual processing. *Nature Reviews. Neuroscience, 14*, 350–363.

- Greenberg, A. S., Esterman, M., Wilson, D., Serences, J. T., & Yantis, S. (2010). Control of spatial and feature-based attention in frontoparietal cortex. *The Journal of Neuroscience*, *30*, 14330–14339.
- Hanslmayr, S., Volberg, G., Wimber, M., Oehler, N., Staudigl, T., Hartmann, T., et al. (2012). Prefrontally driven downregulation of neural synchrony mediates goal-directed forgetting. *The Journal of Neuroscience*, *32*, 14742–14751.
- Heinemann, L., Kleinschmidt, A., & Muller, N. G. (2009). Exploring BOLD changes during spatial attention in non-stimulated visual cortex. *PLoS One*, *4*, e5560.
- Hopf, J. M., Boehler, C. N., Luck, S. J., Tsotsos, J. K., Heinze, H., & Schoenfeld, M. A. (2006). Direct neurophysiological evidence for spatial suppression surrounding the focus of attention in vision. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 1053–1058.
- Huijbers, W., Pennartz, C. M., Cabeza, R., & Daseelaar, S. M. (2009). When learning and remembering compete: A functional MRI study. *PLoS Biology*, *7*, 63–70.
- Jha, A. P., Fabian, S. A., & Aguirre, G. K. (2004). The role of prefrontal cortex in resolving distractor interference. *Cognitive, Affective, & Behavioral Neuroscience*, *4*, 517–527.
- Johnson, M. R., & Johnson, M. K. (2009). Top-down enhancement and suppression of activity in category-selective extrastriate cortex from an act of reflective attention. *Journal of Cognitive Neuroscience*, *21*, 2320–2327.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience*, *17*, 4302–4311.
- Knight, R. T., Staines, W. R., Swick, D., & Chao, L. L. (1999). Prefrontal cortex regulates inhibition and excitation in distributed neural networks. *Acta Psychologica*, *101*, 159–178.
- Kourtzi, Z., & Kanwisher, N. (2001). Representation of perceived object shape by the human lateral occipital complex. *Science*, *293*, 1506–1509.
- Lavie, N. (2005). Distracted and confused?: Selective attention under load. *Trends in Cognitive Sciences*, *9*, 75–82.
- Luck, S. J., Hillyard, S. A., Mouloua, M., Woldorff, M. G., Clark, V. P., & Hawkins, H. L. (1994). Effects of spatial cuing on luminance detectability: Psychophysical and electrophysiological evidence for early selection. *Journal of Experimental Psychology. Human Perception and Performance*, *20*, 887–904.
- Maunsell, J. H. R., & Treue, S. (2006). Feature-based attention in visual cortex. *Trends in Neurosciences*, *29*, 317–322.
- Mevorach, C., Hodsoll, J., Allen, H., Shalev, L., & Humphreys, G. (2010). Ignoring the elephant in the room: A neural circuit to downregulate salience. *The Journal of Neuroscience*, *30*, 6072–6079.
- Miller, B. T., & D'Esposito, M. (2005). Searching for "the top" in top-down control. *Neuron*, *48*, 535–538.
- Minamoto, T., Osaka, M., & Osaka, N. (2010). Individual differences in working memory capacity and distractor processing: Possible contribution of top-down inhibitory control. *Brain Research*, *1335*, 63–73.
- Moher, J., Lakshmanan, B. M., Egeth, H. E., & Ewen, J. B. (2014). Inhibition drives early feature-based attention. *Psychological Science*, *25*, 315–324.
- Moore, T. (2006). The neurobiology of visual attention: Finding sources. *Current Opinion in Neurobiology*, *16*, 159–165.
- Muller, N. G., & Kleinschmidt, A. (2004). The attentional 'spotlight's' penumbra: Center-surround modulation in striate cortex. *Neuroreport*, *15*, 977–980.
- Nelson, J. K., Reuter-Lorenz, P. A., Persson, J., Sylvester, C. Y. C., & Jonides, J. (2009). Mapping interference resolution across task domains: A shared control process in left inferior frontal gyrus. *Brain Research*, *1256*, 92–100.
- Nobre, A. C., Rao, A. L., & Chelazzi, L. (2006). Selective attention to specific features within objects: Behavioral and electrophysiological evidence. *Journal of Cognitive Neuroscience*, *18*, 539–561.
- O'Connor, D. H., Fukui, M. M., Pinsk, M. A., & Kastner, S. (2002). Attention modulates responses in the human lateral geniculate nucleus. *Nature Neuroscience*, *5*, 1203–1209.
- O'Craven, K. M., Downing, P. E., & Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. *Nature*, *401*, 584–587.
- Parks, N. A., Beck, D. M., & Kramer, A. F. (2013). Enhancement and suppression in the visual field under perceptual load. *Frontiers in Psychology*, *4*, 1–8.
- Payne, H. E., & Allen, H. A. (2011). Active ignoring in early visual cortex. *Journal of Cognitive Neuroscience*, *23*, 2046–2058.
- Paz-Alonso, P. M., Bunge, S. A., Anderson, M. C., & Ghetti, S. (2013). Strength of coupling within a mnemonic control network differentiates those who can and cannot suppress memory retrieval. *The Journal of Neuroscience*, *33*, 5017–5026.
- Pinsk, M. A., Doniger, G. M., & Kastner, S. (2004). Push-pull mechanism of selective attention in human extrastriate cortex. *Journal of Neurophysiology*, *92*, 622–629.
- Polk, T. A., Drake, R. M., Jonides, J. J., Smith, M. R., & Smith, E. E. (2008). Attention enhances the neural processing of relevant features and suppresses the processing of irrelevant features in humans: A functional magnetic resonance imaging study of the stroop task. *The Journal of Neuroscience*, *28*, 13786–13792.
- Postle, B. R. (2005). Delay-period activity in the prefrontal cortex: One function is sensory gating. *Journal of Cognitive Neuroscience*, *17*, 1679–1690.
- Pratte, M. S., Ling, S., Swisher, J. D., & Tong, F. (2013). How attention extracts objects from noise. *Journal of Neurophysiology*, *110*, 1346–1356.
- Rissman, J., Gazzaley, A., & D'Esposito, M. (2009). The effect of non-visual working memory load on top-down modulation of visual processing. *Neuropsychologia*, *47*, 1637–1646.
- Ruff, C. C., & Driver, J. (2006). Attentional preparation for a lateralized visual distractor: Behavioral and fMRI evidence. *Journal of Cognitive Neuroscience*, *18*, 522–538.
- Saenz, M., Buracas, G. T., & Boynton, G. M. (2002). Global effects of feature-based attention in human visual cortex. *Nature Neuroscience*, *5*, 631–632.
- Sawaki, R., Geng, J. J., & Luck, S. J. (2012). A common neural mechanism for preventing and terminating the allocation of attention. *The Journal of Neuroscience*, *32*, 10725–10736.
- Sawaki, R., & Luck, S. J. (2013). Active suppression after involuntary capture of attention. *Psychonomic Bulletin & Review*, *20*, 296–301.
- Schenkluhn, B., Ruff, C. C., Heinen, K., & Chambers, C. D. (2008). Parietal stimulation decouples spatial and feature-based attention. *The Journal of Neuroscience*, *28*, 11106–11110.
- Schoenfeld, M. A., Hopf, J. M., Martinez, A., Mai, H. M., Sattler, C., Gasde, A., et al. (2007). Spatio-temporal analysis of feature-based attention. *Cerebral Cortex*, *17*, 2468–2477.
- Seiss, E., Driver, J., & Eimer, M. (2009). Effects of attentional filtering demands on preparatory ERPs elicited in a spatial cueing task. *Clinical Neurophysiology*, *120*, 1087–1095.
- Seiss, E., Gherrri, E., Eardley, A. F., & Eimer, M. (2007). Do ERP components triggered during attentional orienting represent supramodal attentional control? *Psychophysiology*, *44*, 987–990.
- Serences, J. T., & Boynton, G. M. (2007). Feature-based attentional modulations in the absence of direct visual stimulation. *Neuron*, *55*, 301–312.
- Sestieri, C., Shulman, G. L., & Corbetta, M. (2010). Attention to memory and the environment: Functional specialization and dynamic competition in human posterior parietal cortex. *The Journal of Neuroscience*, *30*, 8445–8456.
- Silver, M. A., Ress, D., & Heeger, D. J. (2007). Neural correlates of sustained spatial attention in human early visual cortex. *Journal of Neurophysiology*, *97*, 229–237.
- Slagter, H. A., Giesbrecht, B., Kok, A., Weissman, D. H., Kenemans, J. L., Woldorff, M. G., et al. (2007). AM evidence for both generalized and specialized components of attentional control. *Brain Research*, *1177*, 90–102.
- Slotnick, S. D., Hopfinger, J. B., Klein, S. A., & Sutter, E. E. (2002). Darkness beyond the light: Attentional inhibition surrounding the classic spotlight. *Neuroreport*, *13*, 773–778.
- Sohn, W., Papathomas, T. V., Blaser, E., & Vidnyanszky, Z. (2004). Object-based cross-feature attentional modulation from color to motion. *Vision Research*, *44*, 1437–1443.
- Spreng, R. N., Sepulcre, J., Turner, G. R., Stevens, W. D., & Schacter, D. L. (2013). Intrinsic architecture underlying the relations among the default, dorsal attention, and frontoparietal control networks of the human brain. *Journal of Cognitive Neuroscience*, *25*, 74–86.
- Strumpf, H., Mangun, G. R., Boehler, C. N., Stoppel, C., Schoenfeld, M. A., Heinze, H. J., et al. (2013). The role of the pulvinar in distractor processing and visual search. *Human Brain Mapping*, *34*, 1115–1132.
- Suzuki, M., & Gottlieb, J. (2013). Distinct neural mechanisms of distractor suppression in the frontal and parietal lobe. *Nature Neuroscience*, *16*, 98–104.
- Sylvester, C. M., Jack, A. I., Corbetta, M., & Shulman, G. L. (2008). Anticipatory suppression of nonattended locations in visual cortex marks target location and predicts perception. *The Journal of Neuroscience*, *28*, 6549–6556.
- Toepper, M., Gebhardt, H., Beblo, T., Thomas, C., Driessen, M., Bischoff, M., et al. (2010). Functional correlates of distractor suppression during spatial working memory encoding. *Neuroscience*, *165*, 1244–1253.
- Tootell, R. B. H., Hadjikhani, N., Hall, E. K., Marrett, S., Vanduffel, W., Vaughan, J. T., et al. (1998). The retinotopy of visual spatial attention. *Neuron*, *21*, 1409–1422.
- Valdes-Sosa, M., Bobes, M. A., Rodriguez, V., & Pinilla, T. (1998). Switching attention without shifting the spotlight: Object-based attentional modulation of brain potentials. *Journal of Cognitive Neuroscience*, *10*, 137–151.

- Wais, P., Kim, O., & Gazzaley, A. (2012). Distractibility during episodic retrieval is exacerbated by perturbation of left ventrolateral prefrontal cortex. *Cerebral Cortex*, *22*, 717–724.
- Wais, P., Rubens, M. T., Boccanfuso, J., & Gazzaley, A. (2010). Neural mechanisms underlying the impact of visual distraction on long-term memory retrieval. *The Journal of Neuroscience*, *30*, 8541–8550.
- Zanto, T. P., Chadick, J. Z., Satris, G., & Gazzaley, A. (2013). Rapid functional reorganization in human cortex following neural perturbation. *The Journal of Neuroscience*, *33*, 16268–16274.
- Zanto, T. P., & Gazzaley, A. (2009). Neural suppression of irrelevant information underlies optimal working memory performance. *The Journal of Neuroscience*, *29*, 3059–3066.
- Zanto, T. P., Hennigan, K., Ostberg, M., Clapp, W. C., & Gazzaley, A. (2010). Predictive knowledge of stimulus relevance does not influence top-down suppression of irrelevant information in older adults. *Cortex*, *46*, 561–574.
- Zanto, T. P., Rubens, M. T., Thangavel, A., & Gazzaley, A. (2011). Causal role of the prefrontal cortex in top-down modulation of visual processing and working memory. *Nature Neuroscience*, *14*, 656–661.
- Zanto, T. P., Toy, B., & Gazzaley, A. (2010). Delays in neural processing during working memory encoding in normal aging. *Neuropsychologia*, *48*, 13–25.
- Zhang, W. W., & Luck, S. J. (2009). Feature-based attention modulates feedforward visual processing. *Nature Neuroscience*, *12*, 24–25.