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Top-Down Control of Perceptual Decision Making by the Prefrontal Cortex

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Abstract

Although most work on perceptual decision making has focused on the processing within the visual, temporal, and parietal lobes, recent research points to an underappreciated but critical role of the prefrontal cortex (PFC). PFC provides high-level control of perception, but it is unclear whether this control can be subdivided into different processes and whether different PFC regions have different roles. Here I review evidence that prefrontal top-down control is organized in the processes of selection control, decision control, and evaluation. These three processes overlap and interact with each other while at the same time maintaining a temporal hierarchy. Further, these different stages are supported by dissociable regions within the PFC that control hierarchically organized cognition. The current proposal for PFC's role in perceptual control can serve as the basis for a deeper understanding of both the functional organization of PFC and the processes underlying perceptual decision making.

Keywords

perceptual decision making, prefrontal cortex, top-down, hierarchy, control

You are walking in the woods. All of a sudden, a conspicuous rustling noise comes on your right. You immediately turn to see what caused it and spot a bird sitting on a small bush. However, on the basis of your knowledge of the outdoors, you doubt the rustling noise actually came from the bird. You keep searching, until a moment later you spot a camouflaged snake and immediately escape the scene. How did you find the snake? What processes took place during the brief moments while you searched for the source of the rustling noise?

In a short amount of time, you successfully analyzed a large amount of visual information. To understand how the brain achieves this feat, most of the scientific work on how we visually navigate our environments has focused on the processing within the visual hierarchy starting in the retina and culminating in the extrastriate, temporal, and parietal cortices.

What is typically neglected in this line of research is the role of the prefrontal cortex (PFC) in controlling perceptual decision making. Even though PFC is not directly involved in the analysis of visual information, recent evidence suggests that it plays a critical role in the top-down modulation of perception. Nevertheless, it is still unclear whether this modulation can be subdivided into different processes and, if so, whether these processes are controlled by different PFC areas.

Here I review evidence that PFC control of perceptual decision making can be separated into three hierarchically organized processes. First, PFC controls what the visual system selects for enhanced processing. Second, it controls how the visual system makes a decision about the object's identity and attributes. Finally, PFC evaluates whether the perceptual decision was likely to be correct. The evaluation is then used to determine the next object that is selected for processing, and the cycle is repeated. These three processes are automatically deployed in virtually all perceptual tasks and depend on progressively anterior (i.e., toward the front) regions. In the following sections, I discuss each process, their interrelations, and how they are controlled by PFC.

Selection Control

At any given moment, our perceptual system is bombarded with competing signals, and detailed processing is only possible for a few objects at a time (Peelen &

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Kastner, 2014). Selection of what parts of the scene to process can occur automatically, but salient objects, regardless of their relevance, dominate such selection. Therefore, purposeful search calls for top-down control of the selection process. Most research to date has focused on the processes of spatial, feature-based, or object-level attention (Gilbert & Li, 2013). For our purposes, all of these processes are examples of top-down selection control.

Selection control was repeatedly deployed during your search in the woods. The unexpected noise resulted in a control signal that directed your attention in the general direction of the noise. Once you spotted the bird but determined that it likely did not cause the noise, the selection process was once again directed in a top-down manner until you found the snake.

Decision Control

Once an object is selected for detailed processing, we need to make a decision about its identity or attributes (Heekeren, Marrett, & Ungerleider, 2008). As with selection, this process can proceed automatically but often needs to be modulated in a top-down manner. Top-down control is particularly needed when the decision process has to incorporate nonperceptual information (Rahnev, Lau, & De Lange, 2011; Summerfield & de Lange, 2014) such as prior knowledge or explicit instructions.

Decision control was also repeatedly deployed during your search in the woods. For example, you used prior knowledge of the environment to determine that the colored object on the bush must be a bird and that the rustling noise should have come from the ground.

Evaluation

The decisions that we make are not always correct. We are aware of this fact and can readily evaluate the likely accuracy of our judgments (Metcalfe & Shimamura, 1994). Further, the confidence in our decisions determines our subsequent behavior (Fleming, Dolan, & Frith, 2012; van den Berg, Zylberberg, Kiani, Shadlen, & Wolpert, 2016). In evaluating our decisions, we need to combine the perceptual information with information from context, previous knowledge, etc. (Rahnev, Koizumi, McCurdy, D'Esposito, & Lau, 2015). Just like the control of selection and decision, evaluation is the product of higher level processes (Fleming & Dolan, 2012).

Evaluation was automatically deployed during your search in the woods. For example, you may have had high confidence that the object on the bush was a bird but low confidence in identifying the exact species of bird. Lack of confidence in one's decision often indicates that one should prioritize acquiring additional information. High confidence, on the other hand, generally indicates that one can build and act on the acquired information. Exceptions to this general principle are also possible such as acting to avoid danger even when we are not fully confident a threat exists.

Hierarchical Structure

What is the relationship between selection, decision, and evaluation? When considered together, it becomes clear that these three processes are organized in a temporal hierarchy. Indeed, selection for further processing needs to start before either decision or evaluation can commence (Heekeren et al., 2008). Similarly, the evaluation process cannot start before the decision process (Navajas, Bahrami, & Latham, 2016). Thus, each successive process builds on and extends the previous one. Critically, the control of these processes necessarily follows the temporal structure of the processes themselves (Fig. 1).

Beyond the sequential hierarchy in which lower stages precede and influence the later ones, later stages govern the earlier ones in a top-down manner. For example, previous decisions direct the selection control toward its next target. Similarly, the evaluation determines if the decision processes occurred adequately or if it needs to be repeated by taking into account further information. Finally, the evaluation of the fidelity of a previous decision can also affect what target is selected next such that different selection would take place for the same decision made with high versus low confidence. These top-down influences from the later stages complete the constant loop of visual processing (Fig. 1).

A hierarchical structure does not imply a fully sequential deployment of selection, decision, and evaluation. In particular, although a later process necessarily starts

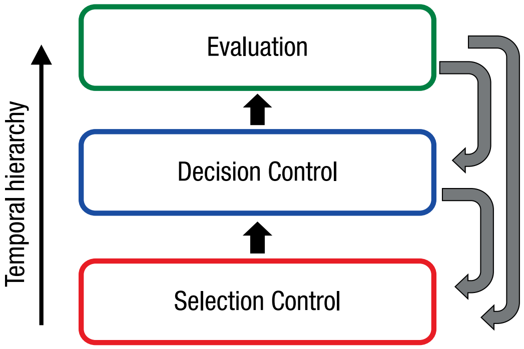

Fig. 1. Temporal hierarchy in top-down control of perception. Selection control, decision control, and evaluation occur in a temporal hierarchy such that the later stages start after and build on the previous stages (black arrows). At the same time, higher levels of the hierarchy control and guide the lower levels (gray arrows).

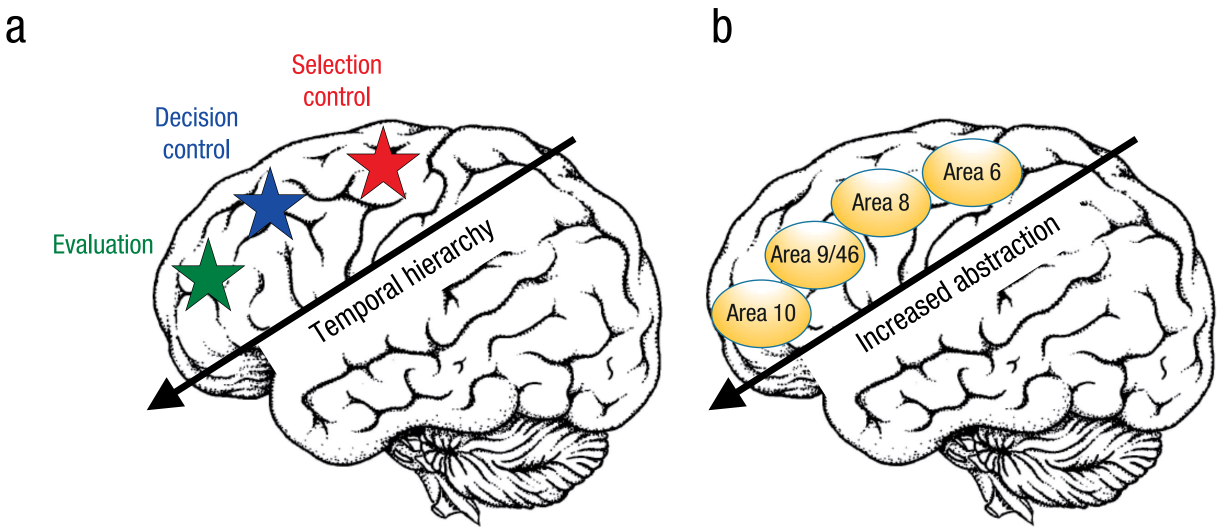

Fig. 2. Temporal hierarchy of perception control in PFC. (a) The location of the areas for selection control (posterior PFC), decision control (mid-PFC), and evaluation (anterior PFC). There is a clear gradient such that later stages of perception control are represented in progressively anterior regions of PFC. (b) The anatomical hierarchy of Brodmann areas that have been theorized to support hierarchically organized cognitive control (Badre & D'Esposito, 2009). The progressively anterior regions from Area 6 to Area 10 are theorized to represent the progressively abstract aspects of cognitive control (Koechlin & Summerfield, 2007).

after the start of an earlier one, its deployment does not need to wait until the end of the earlier process. For example, before selection is fully completed for a new object, decision processes can already start to operate based on nonperceptual information related to the spatial location or individual features of the object. In a similar way, evaluation processes can start before a decision is fully finalized.

The Role of the PFC

The processes of selection control, decision control, and evaluation have been the focus of intense research, but their neural basis has received comparatively less attention. Although many cortical and subcortical regions are involved in these three control processes, here I focus on the role of the PFC. In particular, I argue that progressively anterior areas control the progressively later stages of perceptual decision making.

Previous research generally supports the notion of a posterior-to-anterior PFC gradient in the control of perception. First, a wealth of studies demonstrates that the control of visual attention is mainly exerted by the posterior (i.e., toward the back) PFC (Moore & Zirnsak, 2017). In the case of spatial attention, an area called frontal eye field (FEF) exerts the control (Fig. 2a) by projecting to the visual cortex, which in turn prioritizes the processing of the selected stimulus (Rahnev, Bahdo, de Lange, & Lau, 2012; Vernet, Quentin, Chanes, Mitsumasu, & Valero-Cabré, 2014). Second, several studies suggest that decision control is performed by the middle portion of the PFC called dorsolateral prefrontal cortex (DLPFC; Fig. 2a). For example, DLPFC is critical for the incorporation of nonperceptual information in perceptual decisions (Rahnev et al., 2011; van Veen, Krug, & Carter, 2008). Finally, evaluation signals have been strongly associated with the most anterior part of PFC (Fleming & Dolan, 2012), an area called anterior prefrontal cortex (aPFC; Fig. 2a).

Although the general mapping of later stages of perceptual control to more anterior regions is supported by a number of studies, other research has suggested a less precise map. For example, regions in mid-PFC have been linked to evaluation (Cortese, Amano, Koizumi, Lau, & Kawato, 2016; Rounis, Maniscalco, Rothwell, Passingham, & Lau, 2010) and selection control (Iba & Sawaguchi, 2003), whereas regions in posterior PFC have been associated with decision control (Heitz & Schall, 2012) and evaluation (So & Stuphorn, 2016). Such findings have raised questions as to whether any overarching PFC organization can actually be identified.

To resolve the issue, it is needed to combine the processes of selection control, decision control, and evaluation within a single study, as well as to examine the causal role of different PFC subregions. A recent study (Rahnev, Nee, Riddle, Larson, & D'Esposito, 2016) took exactly this approach. The researchers designed a new task that required subjects to (a) attend to one of two possible stimuli (selection control); (b) switch between speed and accuracy emphasis, thus altering their decision process (decision control); and (c) provide confidence ratings about their decisions (evaluation). The task thus provides a quantitative way to measure each of the three processes independently of each other. The final component of the experimental design was the use of transcranial magnetic stimulation (TMS). The TMS protocol employed, called *continuous theta-burst stimulation*, uses magnetic pulses in order to inhibit local brain function for up to an hour (Huang, Edwards, Rounis, Bhatia, & Rothwell, 2005). The researchers targeted the three frontal regions discussed above—FEF, DLPFC, and aPFC—and compared the effects of TMS to a control condition in which TMS was delivered to a region not involved in the control of visual processing.

The results showed that delivering TMS to FEF (the most posterior PFC region) affected subjects' selection control but had no effect on decision control or evaluation (Rahnev et al., 2016). Moving forward, delivering TMS to DLPFC (the mid-PFC region) primarily affected the ability to modulate the decision process but had no effect on selection and only a small effect on evaluation. Finally, delivering TMS to aPFC (the most anterior region) affected subjects' ability to evaluate their decision but had no effect on their ability to select stimuli or modulate their decision process (Fig. 2a). Taken together, these results provide direct and causal confirmation of the hypothesis that progressively anterior regions of the frontal cortex control progressively later stages of perception. Note that copies of the control signals originating in each PFC subregion could be sent across the PFC and be decoded away from the region in which they originated. This possibility may explain some of the violations of the proposed organization mentioned above (Cortese et al., 2016; Heitz & Schall, 2012; So & Stuphorn, 2016) and points to the need for causal manipulations to pinpoint the origins of each control process.

Relationship to Cognitive Control

The PFC posterior-to-anterior organization in the control of perception has a strong parallel in the cognitive control literature. Very similar organization has been proposed in the hierarchical control of cognition (Badre & D'Esposito, 2009; Fuster, 2008; Koechlin & Summerfield, 2007) such that progressively anterior portions of PFC represent progressively abstract stages of cognition (Fig. 2b). In the cognitive domain, this organization is commonly referred to as rostro-caudal (rostral = anterior; caudal = posterior).

Direct comparison between the PFC organization proposed here and proposals related to cognition (Badre & D'Esposito, 2009; Fuster, 2008; Koechlin & Summerfield, 2007) is made difficult by the heterogeneity of these latter proposals. Nevertheless, what is common among all of these proposals is that PFC forms a hierarchy with later stages situated in more anterior regions. The later stages of the hierarchy build on and control the earlier stages (Fuster, 2008). This structure is the essence of the temporal hierarchy proposed here (Figs. 1 and 2a).

In fact, the posterior-to-anterior organization may be based on the connectivity structure within the PFC itself (Badre & D'Esposito, 2009). Thus, the intrinsic structure of connections within the PFC may explain why very different hierarchies (e.g., in cognitive control and the control of perception) are organized according to the same general principle of posterior-to-anterior representation in PFC.

Future Work

Research on the role of PFC in selection control, decision control, and evaluation has focused primarily on visual processing. It is important for future work to investigate the relationship with other senses such as hearing and somatosensation. Although it is natural to predict that the PFC control for these other senses will overlap in DLPFC and aPFC (decision and evaluation stages), it is likely that separate posterior regions will exert selection control. Indeed, FEF is known to be specialized for spatial visual processing, and recent research has distinguished between neighboring regions in posterior PFC that control visual and auditory information (Michalka, Kong, Rosen, Shinn-Cunningham, & Somers, 2015).

Subsequent research should further investigate the possibility that selection control, decision control, and evaluation themselves consist of other subprocesses. For example, it is possible that spatial and feature-based attention are controlled by separate regions in the posterior PFC (Bichot, Heard, DeGennaro, & Desimone, 2015; Liu & Hou, 2013).

Finally, it is important for future studies to determine more precisely the boundaries between the PFC regions that control different stages of perception. A promising approach would be to apply TMS to multiple narrowly spaced regions along the posterior-to-anterior axis in PFC and observe when the control of each perceptual stage becomes affected.

Conclusion

Although the contribution of visual, temporal, and parietal cortices to visual processing has received a lot of attention, much less is known about the role of the PFC. Recent research suggests that PFC exerts top-down control that is hierarchically organized in the processes of selection control, decision control, and evaluation. These processes are supported by different PFC regions located along a posterior-to-anterior axis. This organization is virtually identical to the PFC organization of the hierarchical control of cognition, and both may be based on PFC's intrinsic anatomical organization. A hierarchical view of the top-down control of perceptual decision making demonstrates the intimate links between perception and cognition and promises to bring deeper insight into each of these domains.

Recommended Reading

Badre, D., & D'Esposito, M. (2009). (See References). An important review of the functional and anatomical evidence for a posterior-to-anterior hierarchy in PFC.

Gilbert, C. D., & Li, W. (2013). (See References). An exhaustive, technical review of the top-down influences in perception focusing on single-cell physiology.

Hasson, U., Chen, J., & Honey, C. J. (2015). Hierarchical process memory: Memory as an integral component of information processing. *Trends in Cognitive Sciences*, *19*, 304–313. An alternative approach to examining hierarchies in the brain through the exploration of the time window over which a region processes information.

Heekeren, H. R., Marrett, S., & Ungerleider, L. G. (2008). (See References). A classical and accessible review of the sensory systems involved in bottom-up processing.

Rahnev, D., Nee, D. E., Riddle, J., Larson, A. S., & D'Esposito, M. (2016). (See References). An empirical report demonstrating the role of PFC in the control of different perceptual stages.

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References

Badre, D., & D'Esposito, M. (2009). Is the rostro-caudal axis of the frontal lobe hierarchical? *Nature Reviews. Neuroscience*, *10*, 659–669. doi:10.1038/nrn2667

Bichot, N. P., Heard, M. T., DeGennaro, E. M., & Desimone, R. (2015). A source for feature-based attention in the prefrontal cortex. *Neuron*, *88*, 832–844. doi:10.1016/j.neuron.2015.10.001

Cortese, A., Amano, K., Koizumi, A., Lau, H., & Kawato, M. (2016). Decoded fMRI neurofeedback can induce bidirectional behavioral changes within single participants. *NeuroImage*, *149*, 323–337. doi:10.1016/j.neuroimage.2017.01.069

Fleming, S. M., & Dolan, R. J. (2012). The neural basis of metacognitive ability. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *367*, 1338–1349. doi:10.1098/rstb.2011.0417

Fleming, S. M., Dolan, R. J., & Frith, C. D. (2012). Metacognition: Computation, biology and function. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *367*, 1280–1286. doi:10.1098/rstb.2012.0021

Fuster, J. M. (2008). *The prefrontal cortex* (4th ed.). London, UK: Academic Press.

Gilbert, C. D., & Li, W. (2013). Top-down influences on visual processing. *Nature Reviews Neuroscience*, *14*, 350–363. doi:10.1038/nrn3476

Heekeren, H. R., Marrett, S., & Ungerleider, L. G. (2008). The neural systems that mediate human perceptual decision making. *Nature Reviews Neuroscience*, *9*, 467–479. doi:10.1038/nrn2374

Heitz, R. P., & Schall, J. D. (2012). Neural mechanisms of speed-accuracy tradeoff. *Neuron*, *76*, 616–628. doi:10.1016/j.neuron.2012.08.030

Huang, Y.- Z., Edwards, M. J., Rounis, E., Bhatia, K. P., & Rothwell, J. C. (2005). Theta burst stimulation of the human motor cortex. *Neuron*, *45*, 201–206. doi:10.1016/j.neuron.2004.12.033

Iba, M., & Sawaguchi, T. (2003). Involvement of the dorsolateral prefrontal cortex of monkeys in visuospatial target selection. *Journal of Neurophysiology*, *89*, 587–599. doi:10.1152/jn.00148.2002

Koechlin, E., & Summerfield, C. (2007). An information theoretical approach to prefrontal executive function. *Trends in Cognitive Sciences*, *11*, 229–235. doi:10.1016/j.tics.2007.04.005

Liu, T., & Hou, Y. (2013). A hierarchy of attentional priority signals in human frontoparietal cortex. *The Journal of Neuroscience*, *33*, 16606–16616. doi:10.1523/JNEUROSCI.1780-13.2013

Metcalfe, J., & Shimamura, A. P. (1994). *Metacognition: Knowing about knowing*. Cambridge, MA: MIT Press.

Michalka, S. W., Kong, L., Rosen, M. L., Shinn-Cunningham, B. G., & Somers, D. C. (2015). Short-term memory for space and time flexibly recruit complementary sensory-biased frontal lobe attention networks. *Neuron*, *87*, 882–892. doi:10.1016/j.neuron.2015.07.028

Moore, T., & Zirnsak, M. (2017). Neural mechanisms of selective visual attention. *Annual Review of Psychology*, *68*, 47–72. doi:10.1146/annurev-psych-122414-033400

Navajas, J., Bahrami, B., & Latham, P. E. (2016). Post-decisional accounts of biases in confidence. *Current Opinion in Behavioral Sciences*, *11*, 55–60. doi:10.1016/j.cobeha.2016.05.005

Peelen, M. V, & Kastner, S. (2014). Attention in the real world: Toward understanding its neural basis. *Trends in Cognitive Sciences*, *18*, 242–250. doi:10.1016/j.tics.2014.02.004

Rahnev, D., Bahdo, L., de Lange, F. P., & Lau, H. (2012). Prestimulus hemodynamic activity in dorsal attention network is negatively associated with decision confidence in visual perception. *Journal of Neurophysiology*, *108*, 1529–1536. doi:10.1152/jn.00184.2012

Rahnev, D., Koizumi, A., McCurdy, L. Y., D'Esposito, M., & Lau, H. (2015). Confidence leak in perceptual decision making. *Psychological Science*, *26*, 1664–1680. doi:10.1177/0956797615595037

Rahnev, D., Lau, H., & De Lange, F. P. (2011). Prior expectation modulates the interaction between sensory and prefrontal regions in the human brain. *Journal of Neuroscience*, *31*, 10741–10748.

Rahnev, D., Nee, D. E., Riddle, J., Larson, A. S., & D'Esposito, M. (2016). Causal evidence for frontal cortex organization for perceptual decision making. *Proceedings of the National Academy of Sciences, USA*, *113*, 6059–6064. doi:10.1073/pnas.1522551113

Rounis, E., Maniscalco, B., Rothwell, J. C., Passingham, R. E., & Lau, H. (2010). Theta-burst transcranial magnetic stimulation to the prefrontal cortex impairs metacognitive visual awareness. *Cognitive Neuroscience*, *1*, 165–175. doi:10.1080/17588921003632529

So, N., & Stuphorn, V. (2016). Supplementary eye field encodes confidence in decisions under risk. *Cerebral Cortex*, *26*, 764–782. doi:10.1093/cercor/bhv025

Summerfield, C., & de Lange, F. P. (2014). Expectation in perceptual decision making: Neural and computational mechanisms. *Nature Reviews Neuroscience*, *15*, 745–756. doi:10.1038/nrn3838

van den Berg, R., Zylberberg, A., Kiani, R., Shadlen, M. N., & Wolpert, D. M. (2016). Confidence is the bridge between multi-stage decisions. *Current Biology*, *26*, 3157–3168. doi:10.1016/j.cub.2016.10.021

van Veen, V., Krug, M. K., & Carter, C. S. (2008). The neural and computational basis of controlled speed-accuracy tradeoff during task performance. *Journal of Cognitive Neuroscience*, *20*, 1952–1965. doi:10.1162/jocn.2008.20146

Vernet, M., Quentin, R., Chanes, L., Mitsumasu, A., & Valero-Cabré, A. (2014). Frontal eye field, where art thou? Anatomy, function, and non-invasive manipulation of frontal regions involved in eye movements and associated cognitive operations. *Frontiers in Integrative Neuroscience*, *8*, 66. doi:10.3389/fnint.2014.00066