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# Representational structures as a unifying framework for attention

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# Abstract

Our visual system consciously processes only a subset of the incoming information. Selective attention allows us to prioritize relevant inputs, and can be allocated to features, locations, and objects. Recent advances in feature-based attention suggest that several selection principles are shared across these domains and that many differences between the effects of attention on perceptual processing can be explained by differences in the underlying representational structures. Moving forward, it can thus be useful to assess how attention changes the structure of the representational spaces over which it operates, which include the spatial organization, feature maps, and object-based coding in visual cortex. This will ultimately add to our understanding of how attention changes the flow of visual information processing more broadly.

# Selection based on features, locations, and objects

To experience a coherent and meaningful world, we must choose what information to prioritize and process. Attention refers to the cognitive function that allows us to select information from the constant stream of sensory inputs and can operate in multiple ways. Attention can be allocated to a specific location in the visual field to prioritize processing of sensory information within the attended region [1]. Attentional selection can also be based on visual features: when looking for your keys on a cluttered desk, you can use their color or shape to help find what you are looking for [2,3]. Finally, attention can operate over entire objects: feature clusters that form a coherent perceptual unit in the visual system [4,5]. While researchers tend to agree that the goal of each of these modes of attention is largely the same (i.e., to select relevant information), there is no consensus on the extent to which the processes supporting selection are shared across these domains, with much work attempting to characterize the mechanisms that distinguish spatial, feature-based, and object-based attention [6–8]. While understanding the differences between them is useful, in our view, it is also important to identify their similarities and integrate across findings with the goal to conceive of a more general framework of selective attention.

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In this Opinion, we review recent findings from the literature on feature-based attention and discuss them in the context of spatial and object-based attention. We focus on the effects of attentional selection on visual processing from the perspective of representational geometry (see Glossary, [9]), to demonstrate that considering the similarity structure of different sensory representations can help reveal shared constraints in attentional selection across domains. In support of this view, we discuss several effects of attention on visual processing, arguing that differences between them are largely due to differences in the underlying structure of the representations in visual cortex, rather than attention itself. The principles discussed here are intended to illustrate the commonalities between different modes of attention, though do not constitute an exhaustive list. Most broadly, we propose that attention can be thought of as a process by which the representational content of information is flexibly shaped in support of adaptive behavior, as opposed to a mechanism that highlights (or filters) particular types of stimuli. This, we believe, will ultimately lead to a more complete model of attention and expand our understanding of how information is transformed across different processing stages in the brain.

# What is feature-based attention?

Feature-based attention refers to the way by which attention can select between different features within a specific feature dimension (e.g., between the colors red and blue) or sometimes also to the selection of one relevant feature dimension over another (e.g., enhancing motion direction over color). Here, we will focus on the selection of one feature among others from the same dimension. (For what can be considered a visual feature; Box 1).

One prominent task used to study feature-based attention is visual search, in which participants are asked to find a target that is usually defined based on a particular visual feature, for example its color, among other nontargets. These tasks nicely map onto how we often use feature-based attention in real-world situations (such as finding a red apple in the fruit section) and have provided important insights into what constrains feature-based selection. For example, the global heterogeneity of the visual scene as well as perceptual similarity between targets and nontargets play a critical role in the efficiency of visual search [10-12], with search times increasing exponentially as the similarity between features increases [13,14]. Models of visual search have promoted the idea of attentional templates that are actively held in working memory and are used to guide search and identify the target (Box 2).

Other research, particularly from the neuroscience literature, has relied on sustained attention tasks as a paradigm for studying feature-based attention [15,16]. In such tasks, groups of stimuli are used to present target and nontarget features at the same spatial location, and different groups of dots comprise a different feature value (e.g., one group is red, another green; one moves upwards, the other downwards, etc.). Because the stimuli are spatially intermingled and change locations randomly, there is no spatial or depth separation to differentiate them. Such tasks provide a useful tool for investigating mechanisms of feature-based attention independently of their ability to guide spatial attention and have been instrumental in showing that feature-based attention can operate in a spatially global way

[15,17]. For example, attention to a specific color or motion direction in one part of the visual field results in increased neural activity to that feature across the entire visual field [15,16,18–20]. Similar to what has been shown for visual search, target-distractor similarity

modulates the efficiency of attentional selection in these sustained attention tasks [13,21], pointing to similar selection limits across these tasks.

# What are the shared principles of feature-based and spatial attention?

Unlike feature-based attention, which is spatially global, spatial attention selects for specific, relevant locations within the visual field, and presumably selects all information within the attended spatial extent (i.e., spatial attention is global for features). That is, spatial and feature-based attention appear to be complementary, and they can be used in combination [22,23]. Like many other visual features (Box 1), space has a defined dimensionality that is relevant to behavior and is encoded within the visual system. Research has shown that regardless of whether selection is based on locations or features, attention can act by increasing sensory gain of attended information, revealing one common mechanism of selection between spatial and feature-based attention [24,25]. Indeed, several models of attention, such as the feature-similarity gain model [16], the theory of visual attention (TVA) [26], as well as the normalization model of attention [27], propose to treat space the same way as other basic visual features. Here we summarize recent empirical work that is consistent with the notion that spatial and feature-based selection can affect visual processing in similar ways, in support of theories of attention that consider both the same way.

#### Time course of spatial and feature-based selection

Starting in the 1980s, the dominant view was that spatial selection has priority over feature-based selection, and although the term priority has often been used rather vaguely, differences in timing (how early processing is affected by attention) and consistency (how reliably processing is affected) were taken as support for this view. For example, electrophysiological studies in humans showed that spatial attention enhances the early visual **P1 component** (~100 ms) [28,29], whereas effects of feature-based attention are often observed later in time (~200 ms post-stimulus onset; the so-called feature-selective negativity) [30–32]. However, studies that continuously presented target and distractor features at the same spatial location to induce high competition found that the early P1 can be increased during feature-based attention as well, and that this increase occurred globally across the visual field [33,34]. While these feature-based P1 effects might be specific to these competitive visual displays and thus more sensitive to task design than early effects of spatial attention [35], these data overall reveal that the selection of visual features can in principle occur as early as selection based on space.

#### Flexible allocation of attention to narrow and broad ranges of features and locations

One key aspect of spatial attention is that it can be flexibly focused on larger or smaller regions in visual space [36–39]. Can feature-based attention similarly zoom in and zoom out in feature space? For example, when the goal is to find apples amongst other fruits, do we attend to one specific color red, or can we tune our attention to ranges of apple-like colors,

such as orange, red, and yellow, at the same time? While this may be less intuitive in the feature domain, if one considers the fact that many features are organized in a map-like structure (Box 1), attention could act on different parts of these feature maps the same way it acts on spatial maps in visual cortex (Figure 1A). Indeed, it has been shown that highly predictive orientation cues elicit a narrower attentional focus and less predictive cues a broader attentional focus in orientation space [40]. Furthermore, in a sustained color-based attention task, participants tuned their attention to broad ranges of colors with only a small decrement in performance [41]. Importantly, in both studies participants attended to the entire range of relevant features relatively uniformly, suggesting that the focus of feature-based attention, just like spatial attention, can flexibly adjust to allocate resources more broadly or narrowly as required by task demands.

#### Selection profile for features and locations

To understand the computational principles of attentional selection it is useful to not only examine how sensory processing changes for attended inputs, but also how unattended and task-irrelevant information processing is modulated. Whereas some studies have found that attentional enhancement gradually falls off as distance from the target increases (in feature space [42] or location space [43]), other studies have shown that selection can elicit an inhibitory zone surrounding the attentional focus, effectively reducing confusability between the attended information and nearby distractors (Figure 1B). That is, attending to red can lead to enhanced processing of red items and attenuated processing of similar relative to less similar colors (e.g., orange vs green). These suppressive surrounds have been observed both in the spatial [44,45] and feature domains [21,46,47], as predicted by the selective tuning (ST) model of attention that proposes center-surround selection as a canonical computation across domains [48,49]. While the exact selection profile of attention appears to depend on task demands and the measurement resolution, recent studies collectively suggest that both gradient and surround inhibition can be implemented both in feature and location space.

#### Perceptual distortions in feature and location space

Feature-based attention has been shown to not always enhance the exact target feature, but in some conditions, enhance neural populations that are tuned away from the target, presumably to increase the signal-to-noise ratio between targets and nontargets [50-52]. For example, when participants are performing an orientation-based [50] or color-based [53] visual search task, they report the target feature to be shifted away from the distractor features in feature space, especially when targets and distractors are similar [52,54]. That is, when selecting a red target among orange distractors, participants report that the target color appears slightly more purple [53]. These perceptual biases due to attention resemble the perceived position shifts of targets in spatial attention tasks, where attending to one location induces the perceived target location to be shifted away from the distractor location [55,56]. Thus, attention to locations and features can lead to perceptual distortions, such that the target is perceived to be pushed away from the distractor representation, ultimately increasing the representational distance between them (Figure 1C) [57]. Broadly, these changes in perception also relate to studies that have demonstrated that spatial attention can alter the appearance of visual stimuli, for example by enhancing the perceived contrast of an attended stimulus to increase discrimination performance [58-61]. Thus, both spatial and

feature-based attention can cause changes in our perceptual experience to support efficient selection.

# How is feature-based attention related to object-based attention?

Research has also suggested that attention can be directed not only towards locations or visual features but towards visual objects. Seminal studies reported that participants are more accurate (or faster) in reporting targets that are superimposed on the same object relative to separate objects [4,62,63], and these behavioral effects are accompanied by neural changes in early visual processing for stimuli appearing at locations within an object relative to between objects [64,65]. Although recent research suggests that these effects are rather small and need large samples to be measured reliably [63], they play a foundational role in theories of object-based attention. However, relative to feature-based and spatial attention, much less is understood about the nature of the object representations in question or even what exactly defines an object with respect to attention. Yet, researchers have suggested that objects are the meaningful unit for attention [66], and that feature-based attention can be thought of as object-based attention [6]. We here take a different stand and suggest that many effects of feature-based selection where enhancement naturally spreads across spatial and feature maps.

#### Perceptual grouping determines spreading of attention

Several studies indicate that perceptual grouping is the key attribute for attention to select more than a single feature (i.e., an object). Specifically, when feature groups overlap spatially [67,68], are perceptually similar [31,69,70], conjoined through uniform connectedness of spatial regions [71], form a surface spanning depth planes [72], or include clear edges [62], attention appears to not just select an isolated singular feature, but rather features associated with that perceptual group [73]. For example, when participants are instructed to attend to a single visual feature - such as the color of a moving stimulus - attention first enhances processing in brain regions that respond to that primary feature (color), but this enhancement subsequently spreads to motion-related regions [67,68,74]. A recent behavioral study demonstrated that spreading of attention between two features at the same location (i.e., attention to red also enhanced the motion direction of these red items) can lead to enhancement of the secondary (never volitionally selected) feature at a different location (i.e., processing of the motion direction was also enhanced in the opposite visual field [70]). A similar effect was found in an electrophysiological study where neurally assessed attention effects spread across hemifields to an initially ignored visual feature of an attended object in the other hemifield [75], revealing that entirely task-irrelevant features receive a processing boost through global spreading of attention. Attention effects also spread across 3D cubes when their surfaces can be grouped (and these effects can be strengthened when connected with another surface, facilitating grouping [76]). This suggests that how attention selects multiple features or locations spontaneously (i.e., without explicit instructions) largely depends on how these features are grouped by the visual system.

#### Attentional enhancement can naturally propagate through feature and spatial maps

As the visual system constantly exploits structured properties of the visual inputs (such as feature similarity or adjacency) because they are likely reflections of distinct objects in the real world [77], perceptual grouping appears to be a straightforward account that can explain several findings in the object-based attention literature. Thus, a more parsimonious definition of object-based attention could be the simple observation of attention spreading between multiple features or locations. This account is agnostic to the theoretical definition of what an object is, a difficult theoretical issue in its own right [66], but rather describes object-based attention as the empirical observation of attention spreading between features. According to this view, object-based effects do not need novel mechanistic explanations of how they occur as they can be readily explained by mechanisms of feature-based attention: Neural populations tuned to different features can be perceptually grouped by the visual system through overlapping spatial receptive fields or similarity within the same feature map, which can provide a scaffolding that allows for attention to spread from one population to another [78]. Reciprocal connections between populations tuned to the same feature at different locations, as well as with higher-level complex visual feature maps can then propagate these attention effects [79]. Thus, while object-based attention is a useful term to describe attentional spreading between features, it does not necessarily require a new mechanistic account.

#### Boundary conditions between feature- and object-based attention

There are, however, also cases where these perceptual grouping processes may not be entirely sufficient to explain object-based attention effects. For example, in multiple-object tracking tasks it has been shown that performance drops dramatically when instead of disks with clear edges, participants are asked to track moving nonsolid substances (that group perceptually but do not have clear boundaries [80]). This indicates that what the attentional system considers to be an object can be more intricate. Furthermore, investigating how attention selects complex real-world objects that entail a multitude of low-level features and also connect to knowledge and semantic meaning can reveal potentially important differences between feature- and object-based attention. For example, research shows that the semantic structure of real-world objects can scaffold how attention is allocated in addition to similarity in low-level feature maps [81]. Thus, investigations of how attention operates over real-world stimuli, which are represented with much higher dimensionality (including visual and semantic dimensions) [82,83], appears especially important and of particular interest within the framework of representational geometry that also incorporates dissimilarity structures for these higher-dimensional spaces (Box 3).

# Towards an integrated framework of attention across features, locations, and objects

As we have outlined in the preceding text, many aspects of attentional selection seem to be shared between spatial, feature-, and object-based attention. This points to the possibility that the differences between these types of attention are based – at least in part – on the fact that they operate over different representational spaces rather than because they truly

reflect different computations or processes. For example, although orientation and color are distinct visual features with different neural representations, differences in the effects of attention on these features do not necessitate that we consider separate orientation-based or color-based attention systems. Likewise, differences in spatial and feature-based attention should not necessarily require separate theories if the differences observed across paradigms can be explained in terms of the underlying representational spaces rather than how attention acts on those representations (Figure 1). It can, of course, still be the case that some features (or feature bundles) are more dominant than others given how their representational architecture is implemented in the visual system (e.g., spatial coding of information is essentially part of any visual representation, and may thus be considered a special class of feature; certain real-world objects (Box 3), such as faces, are potentially unique in how the visual system combines its features, etc.), or because they may be more useful for selection (i.e., more salient due to evolutionary relevance of some features, e.g., color vs orientation); but importantly, these are differences in the representations themselves, and not in how attention acts upon them.

#### Representational spaces and priority maps

This perspective has significant overlap with the literature on priority maps, the idea that attention acts on topographic representations based on the salience or behavioral relevance of particular features [84,85]. Indeed, representational spaces may implement many of the functions of priority maps. One major point of difference is that priority maps are largely defined in terms of retinotopic spatial positions, since these models are primarily predicated on understanding eye movements [86,87]. In comparison, representational spaces in general do not need to be retinotopically organized, so long as the structure of the representations can be extracted from the pattern of activity across neural populations. Map-like structures have previously been put forward as a way to understand processing limits in attention and working memory [88], and point towards understanding how the visual system groups and partitions different inputs as a key step towards characterizing cognitive capacities. For example, research has demonstrated that Gestalt properties, such as similarity, collinearity, and common fate can act as scaffolds to allow for the spreading of activation from one item to another [78]. Indeed, similarity between stimuli (e.g., in spatial position or feature space) may provide a common scale for attentional selection, indexing the representational overlap between different sources of information.

#### Attention sculpts representational spaces

Once one considers explicitly the organization of the different representational spaces, it also becomes important to understand how selective processing affects these representational spaces as a whole. For example, in our recent work we found that selecting a target color distorts the representational feature space in a way that separates targets and distractors and, critically, these attention-induced shifts had downstream consequences across large swaths of the rest of the feature space [53] (Figure 2A). This demonstrates that selection does not just affect the representational space. Such warping due to attention has also been observed for location [55,56] (Figure 2B), as well as more complex and higher-level dimensions, such as semantic categories (Figure 2C), where attention acts to separate neural

population responses along the behaviorally relevant dimension, resulting in distortions of the underlying representational structure [89,90]. Along a similar vein, recent computational approaches have explored how activity in neural systems follows dynamic and flexible trajectories during working memory and decision making [91,92]. Potentially, changes in the representational structure under attention may help shape these dynamics, essentially forging a pathway for relevant information to flow more efficiently (i.e., by aligning communication subspaces) [93,94]. Thus, attention does not only influence processing of information at the attended location or feature, but instead can sculpt the entire representational geometry in a way to best support behavior. These changes in representational structure can occur across location and feature spaces, including groups of feature representational spaces – their organization, structure, and flexibility – and how attention changes them, is a critical step towards explaining attentional selection and its limits.

### **Concluding remarks**

Research on visual selective attention, in particular recent findings in feature-based attention, has revealed several similarities between what is often referred to as spatial, feature-, and object-based attention. Thus, these modes of attention appear less distinct than often portrayed in the literature, although there are important boundary conditions that may distinguish them (e.g., tracking, real-world objects). Here, we want to encourage researchers to look beyond the differences and shift the focus towards considering the structure and constraints of our mental representational spaces (locations, simple visual features such as orientation or color, or higher-level feature spaces such as faces, objects, or conceptual knowledge), and how attention affects these structures. This will ultimately help us understand the nature of our processing limits and abilities (see Outstanding Questions).

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# Glossary

#### **Attentional templates**

visual features that are maintained in working memory because they are relevant for a current task

#### Guidance

process of attention being directed to stimuli that are most likely to be the target, which can be due to the saliency of a stimulus, the implicit or explicit goals of an observer, prior experience, scene structure, etc

#### P1 component

first positive-going deflection of the scalp-recorded event-related potential collected by means of electroencephalography. It usually occurs ~100 ms after the presentation of a visual stimulus and is thought to stem from extrastriate areas of the visual cortex

#### **Priority map**

model representing the priority of stimuli at different points in an abstract map in a given stimulus space. Traditionally, in the visual domain, this map represents 2D spatial locations, with the activation level at a given location denoting that location's priority

#### **Representational geometry**

framework that allows us to relate brain, computation, and cognition by characterizing mental representations in terms of their dissimilarities based on the neural response patterns of a set of stimuli

#### Search slope

search slopes (ms/item) in visual search tasks indicate the average increase in response times due to each added item on the display. A smaller search slope is indicative of a more efficient search

#### Sustained attention task

these tasks require participants to continuously maintain their focus of attention on a certain location or feature among irrelevant locations/features for an extended period of time (e.g., several seconds). To ensure participants are persistently attending to the relevant items, they often monitor for the brief occurrence of a target event, for example a change in luminance of the to-be-attended location/feature

#### Visual search

task of looking for something in a cluttered visual environment. The stimulus that people are looking for is termed the target, and the other items are termed nontargets or distractors

#### References

- 1. Posner MI (1980) Orienting of attention. Q. J. Exp. Psychol 32, 3-25 [PubMed: 7367577]
- Driver J and Baylis GC (1989) Movement and visual attention: the spotlight metaphor breaks down. J. Exp. Psychol. Hum. Percept. Perform 15, 448–456 [PubMed: 2527954]
- Maunsell JHR and Treue S (2006) Feature-based attention in visual cortex. Trends Neurosci 29, 317–322 [PubMed: 16697058]
- Duncan J (1984) Selective attention and the organization of visual information. J. Exp. Psychol. Gen 113, 501–517 [PubMed: 6240521]
- O'Craven KM et al. (1999) fMRI evidence for objects as the units of attentional selection. Nature 401, 584–587 [PubMed: 10524624]
- Cavanagh P et al. (2023) The architecture of object-based attention. Psychon. Bull. Rev 30, 1643– 1667 [PubMed: 37081283]
- Ibos G and Freedman DJ (2016) Interaction between spatial and feature attention in posterior parietal cortex. Neuron 91, 931–943 [PubMed: 27499082]
- Liu T and Hou Y (2013) A hierarchy of attentional priority signals in human frontoparietal cortex. J. Neurosci 33, 16606–16616 [PubMed: 24133264]
- Kriegeskorte N and Wei XX (2021) Neural tuning and representational geometry. Nat. Rev. Neurosci 22, 703–718 [PubMed: 34522043]
- Duncan J and Humphreys GW (1989) Visual search and stimulus similarity. Psychol. Rev 96, 433–458 [PubMed: 2756067]
- Geng JJ and Witkowski P (2019) Template-to-distractor distinctiveness regulates visual search efficiency. Curr. Opin. Psychol 29, 119–125 [PubMed: 30743200]
- 12. Wolfe JM (2023) Visual search, Oxford Research Encyclopedia of Psychology

- Chapman AF and Störmer VS (2022) Feature similarity is non-linearly related to attentional selection: evidence from visual search and sustained attention tasks. J. Vis 22, 4
- Buetti S et al. (2016) Towards a better understanding of parallel visual processing in human vision: evidence for exhaustive analysis of visual information. J. Exp. Psychol. Gen 145, 672–707 [PubMed: 27077758]
- Sàenz M et al. (2002) Global effects of feature-based attention in human visual cortex. Nat. Neurosci 5, 631–632 [PubMed: 12068304]
- Treue S and Martinez-Trujillo JC (1999) Feature-based attention influences motion processing gain in macaque visual cortex. Nature 399, 575–579 [PubMed: 10376597]
- 17. White AL and Carrasco M (2011) Feature-based attention involuntarily and simultaneously improves visual performance across locations. J. Vis 11, 1–10
- Andersen SK et al. (2013) Global facilitation of attended features is obligatory and restricts divided attention. J. Neurosci 33, 18200–18207 [PubMed: 24227728]
- Serences JT and Boynton GM (2007) Feature-based attentional modulations in the absence of direct visual stimulation. Neuron 55, 301–312 [PubMed: 17640530]
- Lustig AG and Beck DM (2012) Task-relevant and task-irrelevant dimensions are modulated independently at a task-irrelevant location. J. Cogn. Neurosci 24, 1884–1895 [PubMed: 22624607]
- Störmer VS and Alvarez GA (2014) Feature-based attention elicits surround suppression in feature space. Curr. Biol 24, 1985–1988 [PubMed: 25155510]
- 22. Liang G et al. (2023) Space and feature-based attention operate both independently and interactively within latent components of perceptual decision making. J. Vis 23, 1–17
- 23. Hayden BY and Gallant JL (2009) Combined effects of spatial and feature-based attention on responses of V4 neurons. Vis. Res 49, 1182–1187 [PubMed: 18619996]
- 24. Ling S et al. (2009) How spatial and feature-based attention affect the gain and tuning of population responses. Vis. Res 49, 1194–1204 [PubMed: 18590754]
- 25. Hillyard SA et al. (1998) Sensory gain control (amplification) as a mechanism of selective attention: electrophysiological and neuroimaging evidence. Philos. Trans. R. Soc. B Biol. Sci 353, 1257–1270
- 26. Bundesen C (1990) A theory of visual attention. Psychol. Rev 97, 523–547 [PubMed: 2247540]
- 27. Reynolds JH and Heeger DJ (2009) The normalization model of attention. Neuron 61, 168–185 [PubMed: 19186161]
- Clark VP and Hillyard SA (1996) Spatial selective attention affects early extrastriate but not striate components of the visual evoked potential. J. Cogn. Neurosci 8, 387–402 [PubMed: 23961943]
- Luck SJ et al. (1990) Visual event-related potentials index focused attention within bilateral stimulus arrays. II. Functional dissociation of P1 and N1 components. Electroencephalogr. Clin. Neurophysiol 75, 528–542 [PubMed: 1693897]
- Anllo-Vento L and Hillyard SA (1996) Selective attention to the color and direction of moving stimuli: Electrophysiological correlates of hierarchical feature selection. Percept. Psychophys 58, 191–206 [PubMed: 8838164]
- Bartsch MV et al. (2018) Enhanced spatial focusing increases feature-based selection in unattended locations. Sci. Rep 8, 1–14 [PubMed: 29311619]
- Bartsch MV et al. (2017) Attention to color sharpens neural population tuning via feedback processing in the human visual cortex hierarchy. J. Neurosci 37, 10346–10357 [PubMed: 28947573]
- Zhang W and Luck SJ (2009) Feature-based attention modulates feedforward visual processing. Nat. Neurosci 12, 24–25 [PubMed: 19029890]
- 34. Moher J et al. (2014) Inhibition drives early feature-based attention. Psychol. Sci 25, 315–324 [PubMed: 24390823]
- 35. Liu T et al. (2007) Comparing the time course and efficacy of spatial and feature-based attention. Vis. Res 47, 108–113 [PubMed: 17087987]
- Eriksen CW and St. James JD (1986) Visual attention within and around the field of focal attention. Percept. Psychophys 40, 225–240 [PubMed: 3786090]

- Herrmann K et al. (2010) When size matters: attention affects performance by contrast or response gain. Nat. Neurosci 13, 1554–1561 [PubMed: 21057509]
- 38. Itthipuripat S et al. (2014) Changing the spatial scope of attention alters patterns of neural gain in human cortex. J. Neurosci 34, 112–123 [PubMed: 24381272]
- Intriligator J and Cavanagh P (2001) The spatial resolution of visual attention. Cogn. Psychol 43, 171–216 [PubMed: 11689021]
- Herrmann K et al. (2012) Feature-based attention enhances performance by increasing response gain. Vis. Res 74, 10–20 [PubMed: 22580017]
- 41. Chapman AF and Störmer VS (2023) Flexible focus in feature-based attention: efficient tuning of attention to narrow and broad ranges of task-relevant feature values. Vis. Cogn 31, 63–84
- 42. Martinez-Trujillo JC and Treue S (2004) Feature-based attention increases the selectivity of population responses in primate visual cortex. Curr. Biol 14, 744–751 [PubMed: 15120065]
- Mangun GR and Hillyard SA (1988) Spatial gradients of visual attention: behavioral and electrophysiological evidence. Electroencephalogr. Clin. Neurophysiol 70, 417–428 [PubMed: 2460315]
- 44. Boehler CN et al. (2011) Neural mechanisms of surround attenuation and distractor competition in visual search.J. Neurosci 31, 5213–5224 [PubMed: 21471356]
- 45. Hopf J-MM et al. (2006) Direct neurophysiological evidence for spatial suppression surrounding the focus of attention in vision. Proc. Natl. Acad. Sci 103, 1053–1058 [PubMed: 16410356]
- 46. Fang MWH and Liu T (2019) The profile of attentional modulation to visual features. J. Vis 19, 1–16
- 47. Yoo SA et al. (2022) Attention to visual motion suppresses neuronal and behavioral sensitivity in nearby feature space. BMC Biol 20, 1–19 [PubMed: 34983491]
- 48. Cutzu F and Tsotsos JK (2003) The selective tuning model of attention: psychophysical evidence for a suppressive annulus around an attended item. Vis. Res 43, 205–219 [PubMed: 12536142]
- 49. Tsotsos JK et al. (1995) Modeling visual attention via selective tuning. Artif. Intell 78, 507-545
- 50. Navalpakkam V and Itti L (2007) Search goal tunes visual features optimally. Neuron 53, 605–617 [PubMed: 17296560]
- Scolari M and Serences JT (2009) Adaptive allocation of attentional gain. J. Neurosci 29, 11933– 11942 [PubMed: 19776279]
- Kerzel D (2020) Direct evidence for the optimal tuning of attention. J. Exp. Psychol. Hum. Percept. Perform 46, 716–728 [PubMed: 32271080]
- 53. Chapman AF et al. (2023) Feature-based attention warps the perception of visual features. Sci. Rep 13, 6487 [PubMed: 37081047]
- Martinovic J et al. (2018) Neural mechanisms of divided feature-selective attention to colour. Neuroimage 181, 670–682 [PubMed: 30048748]
- 55. Suzuki S and Cavanagh P (1997) Focused attention distorts visual space: an attentional repulsion effect. J. Exp. Psychol. Hum. Percept. Perform 23, 443–463 [PubMed: 9104004]
- Pratt J and Turk-Browne NB (2003) The attentional repulsion effect in perception and action. Exp. Brain Res 152, 376–382 [PubMed: 12928759]
- 57. Mehrpour V et al. (2020) Attention amplifies neural representations of changes in sensory input at the expense of perceptual accuracy. Nat. Commun 11, 2128 [PubMed: 32358494]
- Carrasco M et al. (2004) Attention alters appearance. Nat. Neurosci 7, 308–313 [PubMed: 14966522]
- 59. Fuller S and Carrasco M (2006) Exogenous attention and color perception: performance and appearance of saturation and hue. Vis. Res 46, 4032–4047 [PubMed: 16979690]
- Störmer VS and Alvarez GA (2016) Attention alters perceived attractiveness. Psychol. Sci 27, 563–571 [PubMed: 26966228]
- Störmer VS et al. (2009) Cross-modal cueing of attention alters appearance and early cortical processing of visual stimuli. Proc. Natl. Acad. Sci. U. S. A 106, 22456–22461 [PubMed: 20007778]
- 62. Egly R et al. (1994) Shifting visual attention between objects and locations: evidence from normal and parietal lesion subjects. J. Exp. Psychol. Gen 123, 161–177 [PubMed: 8014611]

- 63. Francis G and Thunell E (2022) Excess success in articles on object-based attention. Atten. Percept. Psychophys 84, 700–714 [PubMed: 35233745]
- 64. Martinez A et al. (2007) The role of spatial attention in the selection of real and illusory objects. J. Neurosci 27, 7963–7973 [PubMed: 17652587]
- 65. Ekman M et al. (2020) Object selection by automatic spreading of top-down attentional signals in V1. J. Neurosci 40, 9250–9259 [PubMed: 33087475]
- 66. Scholl BJ (2001) Objects and attention: the state of the art. Cognition 80, 1–46 [PubMed: 11245838]
- 67. Ernst ZR et al. (2013) The spread of attention across features of a surface. J. Neurophysiol 110, 2426–2439 [PubMed: 23883860]
- Schoenfeld MA et al. (2014) Object-based attention involves the sequential activation of featurespecific cortical modules. Nat. Neurosci 17, 619–624 [PubMed: 24561999]
- Adamian N et al. (2019) Top–down attention is limited within but not between feature dimensions. J. Cogn. Neurosci 31, 1173–1183 [PubMed: 30794058]
- Chapman AF and Störmer VS (2021) Feature-based attention is not confined by object boundaries: Spatially global enhancement of irrelevant features. Psychon. Bull. Rev 28, 1252–1260 [PubMed: 33687666]
- 71. Palmer S and Rock I (1994) Rethinking perceptual organization: the role of uniform connectedness. Psychon. Bull. Rev 1, 29–55 [PubMed: 24203413]
- He ZJ and Nakayama K (1995) Visual attention to surfaces in three-dimensional space. Proc. Natl. Acad. Sci. U. S. A 92, 11155–11159 [PubMed: 7479956]
- 73. Valdes-Sosa M et al. (1998) Switching attention without shifting the spotlight: object-based attentional modulation of brain potentials. J. Cogn. Neurosci 10, 137–151 [PubMed: 9526088]
- 74. Roelfsema PR et al. (1998) Object-based attention in the primary visual cortex of the macaque monkey. Nature 395, 376–381 [PubMed: 9759726]
- 75. Boehler CN et al. (2011) Object-based selection of irrelevant features is not confined to the attended object. J. Cogn. Neurosci 23, 2231–2239 [PubMed: 20666592]
- 76. Erlikhman G et al. (2020) Object-based attention generalizes to multisurface objects. Atten. Percept. Psychophys 82, 1599–1612 [PubMed: 31919757]
- 77. Wertheimer M (1923) Laws of organization in perceptual forms. Psychol. Forsch 4, 301-350
- 78. Wannig A et al. (2011) Automatic spread of attentional response modulation along Gestalt criteria in primary visual cortex. Nat. Neurosci 14, 1243–1244 [PubMed: 21926984]
- 79. Duncan J et al. (1997) Competitive brain activity in visual attention. Curr. Opin. Neurobiol 7, 255–261 [PubMed: 9142748]
- VanMarle K and Scholl BJ (2003) Attentive tracking of objects versus substances. Psychol. Sci 14, 498–504 [PubMed: 12930483]
- Shomstein S et al. (2019) Intrusive effects of task-irrelevant information on visual selective attention: semantics and size. Curr. Opin. Psychol 29, 153–159 [PubMed: 30925285]
- 82. Long B et al. (2018) Mid-level visual features underlie the high-level categorical organization of the ventral stream. Proc. Natl. Acad. Sci 115, E9015–E9024 [PubMed: 30171168]
- 83. Hebart MN et al. (2020) Revealing the multidimensional mental representations of natural objects underlying human similarity judgements. Nat. Hum. Behav 4, 1173–1185 [PubMed: 33046861]
- Bisley JW and Mirpour K (2019) The neural instantiation of a priority map. Curr. Opin. Psychol 29, 108–112 [PubMed: 30731260]
- Serences JT and Yantis S (2006) Selective visual attention and perceptual coherence. Trends Cogn. Sci 10, 38–45 [PubMed: 16318922]
- Itti L and Koch C (2001) Computational modelling of visual attention. Nat. Rev. Neurosci 2, 194–203 [PubMed: 11256080]
- Bichot NP and Schall JD (1999) Effects of similarity and history on neural mechanisms of visual selection. Nat. Neurosci 2, 549–554 [PubMed: 10448220]
- Franconeri SL et al. (2013) Flexible cognitive resources: competitive content maps for attention and memory. Trends Cogn. Sci 17, 134–141 [PubMed: 23428935]

- Çukur T et al. (2013) Attention during natural vision warps semantic representation across the human brain. Nat. Neurosci 16, 763–770 [PubMed: 23603707]
- Nastase SA et al. (2017) Attention selectively reshapes the geometry of distributed semantic representation. Cereb. Cortex 27, 4277–4291 [PubMed: 28591837]
- 91. Meyers EM (2018) Dynamic population coding and its relationship to working memory. J. Neurophysiol 120, 2260–2268 [PubMed: 30207866]
- 92. Stokes MG et al. (2013) Dynamic coding for cognitive control in prefrontal cortex. Neuron 78, 364–375 [PubMed: 23562541]
- Ruff DA et al. (2018) Cognition as a window into neuronal population space. Annu. Rev. Neurosci 41, 77–97 [PubMed: 29799773]
- 94. Rust NC and Cohen MR (2022) Priority coding in the visual system. Nat. Rev. Neurosci 23, 376–388 [PubMed: 35410358]
- Hubel DH and Wiesel TN (1968) Receptive fields and functional architecture of monkey striate cortex. J. Physiol 195, 215–243 [PubMed: 4966457]
- 96. Roth ZN et al. (2022) Natural scene sampling reveals reliable coarse-scale orientation tuning in human V1. Nat. Commun 13, 6469 [PubMed: 36309512]
- 97. Albright TD et al. (1984) Columnar organization of directionally selective cells in visual area MT of the macaque. J. Neurophysiol 51, 16–31 [PubMed: 6693933]
- Bohon KS et al. (2016) Representation of perceptual color space in macaque posterior inferior temporal cortex (The V4 complex). eNeuro 3
- Conway BR et al. (2007) Specialized color modules in macaque extrastriate cortex. neuron 56, 560–573 [PubMed: 17988638]
- 100. Shepard RN (1987) Toward a universal law of generalization for psychological science. Science (80-. ) 237, 1317–1323
- 101. Brouwer GJ and Heeger DJ (2009) Decoding and reconstructing color from responses in human visual cortex.J. Neurosci 29, 13992–14003 [PubMed: 19890009]
- 102. Wolfe JM and Utochkin IS (2019) What is a preattentive feature? Curr. Opin. Psychol 29, 19–26 [PubMed: 30472539]
- 103. Wolfe JM and Horowitz TS (2017) Five factors that guide attention in visual search. Nat. Hum. Behav 1, 1-8
- 104. Witkowski PP and Geng JJ (2022) Attentional priority is determined by predicted feature distributions. J. Exp. Psychol. Hum. Percept. Perform 48, 1201–1212 [PubMed: 36048065]
- 105. Yu X and Geng JJ (2019) The attentional template is shifted and asymmetrically sharpened by distractor context. J. Exp. Psychol. Hum. Percept. Perform 45, 336–353 [PubMed: 30742475]
- 106. Hamblin-Frohman Z and Becker SI (2021) The attentional template in high and low similarity search: Optimal tuning or tuning to relations? Cognition 212, 104732 [PubMed: 33862440]
- 107. Rajsic J and Woodman GF (2019) Do we remember templates better so that we can reject distractors better? Atten. Percept. Psychophys 82, 269–279
- 108. Wolfe JM (2021) Guided Search 6. 0: an updated model of visual search. Psychon. Bull. Rev 28, 1060–1092 [PubMed: 33547630]
- 109. Yu X et al. (2023) Good-enough attentional guidance. Trends Cogn. Sci 27, 391–403 [PubMed: 36841692]
- 110. Williams JR et al. (2022) Guidance of attention by working memory is a matter of representational guidance of attention by working memory is a matter of representational fidelity. J. Exp. Psychol. Hum. Percept. Perform 48, 202–231 [PubMed: 35084932]
- 111. Najemnik J and Geisler WS (2005) Optimal eye movement strategies in visual search. Nature 434, 387–391 [PubMed: 15772663]
- Tong F et al. (1998) Binocular rivalry and visual awareness in human extrastriate cortex. Neuron 21, 753–759 [PubMed: 9808462]
- 113. Peelen MV and Kastner S (2014) Attention in the real world: toward understanding its neural basis. Trends Cogn. Sci 18, 242–250 [PubMed: 24630872]
- 114. Störmer VS et al. (2019) Tuning attention to object categories: spatially global effets of attention to faces in visual processing.J. Cogn. Neurosci 31, 937–947 [PubMed: 30912729]

- 115. Hwang AD et al. (2011) Semantic guidance of eye movements in real-world scenes. Vis. Res 51, 1192–1205 [PubMed: 21426914]
- 116. Addleman DA et al. (2022) Attention to object categories: selection history determines the breadth of attentional tuning during real-world object search. PsyArxiv, Published online October 20, 2022. 10.31234/osf.io/s8nyz

# Highlights

Selective attention is often studied separately as spatial, feature-based, and object-based attention.

Recent research on feature-based attention in particular demonstrates that many selection principles are shared across these domains, suggesting that a core set of mechanisms supports effective information processing in the human brain, regardless of domain.

Understanding the underlying representational structures, such as the spatial organization, various feature spaces, and object-based coding in visual cortex, will aid unifying theories of attention.

Considering the structures of perceptual representations will also open up the possibility to study how selection sculpts entire representational spaces to support efficient information processing.

#### **Outstanding questions**

How does attentional selection change representational geometry? How can changes in representational structure be measured and modeled?

Is there a canonical limit on how broadly (or narrowly) attention can be tuned across different feature spaces once differences in the representational structures (i.e., perceptual similarity) is accounted for?

Are there differences in surround-suppression for different feature dimensions? Peak suppressive regions might occur at consistent spots across different feature maps once perceptual similarity is considered. At the same time, how would individual differences in perceptual spaces, or changes over time (e.g., through perceptual training and expertise) affect selection limits?

What is the organizational structure of more complex and abstract feature spaces, and do similar selection principles apply in these higher-dimensional spaces (e.g., real-world objects, conceptual knowledge)?

If representational spaces accurately capture attentional selection for visual stimuli, do these same principles extend to other sensory modalities? What is the representational structure of auditory or tactile stimuli, for example, and how does attention function in these modes?

#### Box 1.

#### What is a visual feature?

A visual feature is most clearly defined in the context of visual feature detectors: individual neurons or groups of neurons that selectively respond to perceptually significant stimuli in the visual world. Beginning in the 1960s and 1970s, neurophysiological recordings identified neural populations tuned to specific visual features, such as motion direction, spatial frequency, stereoscopic depth, color, or orientation (e.g., [95]). Importantly, these features are encoded independently, indicating that they reflect separate and orthogonal feature dimensions (e.g., orientation can change independently of color). Several neurophysiological studies showed that neurons within a feature dimension are organized in a map-like structure where similar features are represented near each other. For example, there are maps of orientation in V1 [95,96], motion direction in hMT/V5 [97], or color in ventral visual cortex [98,99]. The structure of these neural representations also directly relates to the psychological structure of the feature space, as reflected through the effects of similarity on perceptual performance: features that are near each other (and thus more similar) in the representational space are also responded to in more similar ways than more distinct features (i.e., stimulus generalization) [16,100]. While this correspondence may not exist across all processing stages of the visual hierarchy – color is represented in terms of opponentprocesses at early levels, but then this representation becomes more reflective of the psychological representation later on in the visual cortex [99,101] – organized maps that are concordant with the perceptually relevant dimensions pose an intriguing format for feature representations. Finally, the psychologically relevant structure of features can be well represented in terms of dimensionality of a feature: one dimension for orientation  $(0-180^\circ)$  and motion direction  $(0-360^\circ)$ , or three dimensions for color (hue, saturation, and luminance, for one – although certainly not the only – representational space). Thus, several visual features have been well described in terms of their physiology, neural structure, and psychological representation. Based on this, researchers have also compiled lists of what features are in terms of attention, or more specifically which features may guide spatial attention [102,103].

#### Box 2.

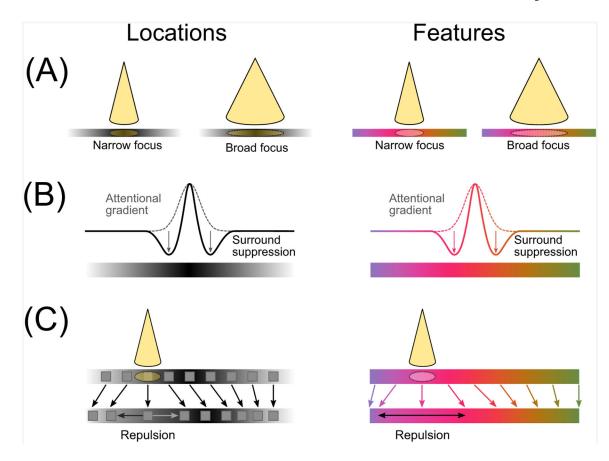
## Attentional templates during feature-based attention

In visual search, participants are often required to hold a target feature actively in working memory to then find that target feature in a cluttered visual display. These template-based visual search tasks resemble how we often look for a particular item in the real world and have been of interest to attention researchers for a long time. Recent research indicates that these templates can adapt to the search context flexibly, for example by tracking target feature probabilities [104] and also by shifting resources away from consistent nontarget features [105,106]. In addition, it has been suggested that attentional guidance (e.g., measured in terms of eye movements or search slopes) might rely on a coarser template (e.g., warm colors) than perceptual decisions about target identification (i.e., the exact red held in mind; measured as accuracy in identifying the true target feature, or an overall change in response times independently of set size; [107–109]). While different measures (accuracy in reporting a feature vs. response times or eye movements) can produce different patterns of performance in visual search, it remains to be determined how each of these measures maps onto the proposed cognitive processes. Indeed, recent research has demonstrated that the amount of guidance during search is perfectly predicted by the representational fidelity of the target item in memory, indicating that the same representation underlies both [110]. Future work can build on this further, for example by comparing performance more directly to computational models that more explicitly define these aspects of visual search (e.g., ideal observer models; [111]).

#### Box 3.

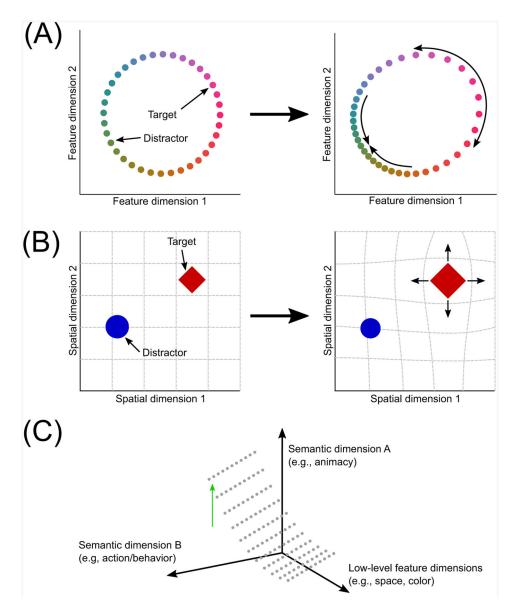
#### Attention to real-world objects

Several studies on object-based attention use images of real-world objects - such as faces, houses, cars, or bodies – and show that attention can be directed to these realworld objects and enhance their processing holistically [5,112]. For example, studies demonstrated that when participants attended to faces overlaid on houses to detect a brief motion of the attended stimuli, neural responses in category-selective visual cortex corresponding to the attended objects were enhanced relative to the unattended object (fusiform face areas and parahippocampal place area, respectively). In other cases, participants were asked to search for people or cars in real-world scene images, and neural processing was enhanced for these object categories across the visual field, in agreement with spatially global object-based selection [113]. Similarly, when participants attended to faces at one location in the visual field, processing of faces at another task-irrelevant location was selectively enhanced [114], again suggesting that tuning attention to an object category can enhance visual processing of that category across the visual field. In our view, many of these attention effects on real-world objects can be readily explained within the perceptual grouping framework discussed in the main text. However, in the case of meaningful, real-world objects that are represented not only in terms of their lower-level visual features but also in terms of higher-level visual and semantic features that connect to preexisting knowledge (e.g., categories and familiarity), attentional selection is constrained across all these processing levels, including low- and mid-level visual similarity and higher-level semantic similarity. Thus, semantic and conceptual knowledge can provide an additional, and potentially particularly effective, scaffolding of how attention is allocated across real-world stimuli. Studies have shown, for example, that people's eye movements are guided towards objects that are semantically related to a target object (e.g., when searching for a fork, people are likely to also look at a knife [115]). Furthermore, a recent study demonstrated that when participants are incidentally learning to attend to specific objects from the same category, attention spreads to other novel objects from the same category [116]. Some of these categorical effects are likely shaped by the large-scale organization in higher-level visual cortex that covaries meaningfully with lower-level and in particular mid-level visual features [82], and could thus be considered a continuation of the lower-level feature maps; future studies should take this into account when investigating attention to real-world stimuli.



#### Figure 1. Selection principles across location and feature space.

(A) Locations and features are represented nearby each other in a map-like structure. The focus of attention can be tuned narrowly and broadly to select information over a small or large spatial region within the map (left), or small or large ranges of feature values (right).
(B) When a specific location or feature is selected by attention, this can enhance processing of the target, with this enhancement falling off gradually (attentional gradient – broken line); but selection can also elicit a suppressive surround around the focus of attention, for example through lateral connections in location or feature maps. (C) Selection can lead to distortions in location or feature space, for example by increasing the representational distance between the selected target and surrounding representations (repulsion).



#### Figure 2. Selective attention can induce changes in representational geometry.

(A) When a target is selected among a distractor, this may not only change processing of the target and distractor representations (e.g., by increasing or decreasing neural gain, respectively), but this may also lead to alterations in the entire feature space, for example by expanding the distance between features in one part of the space and compressing the feature representations in another part of the space. (B) Such changes in representational geometry can occur in any feature space, including spatial representations. (C) Representational geometry may also help explain the effects of attention on high-dimensional object representations. For example, attending to animate over inanimate objects may expand representations along the animacy dimension, resulting in a greater distance between objects as a function of their perceived animacy.