Opinion

Peripheral and central sensation: multisensory orienting and recognition across species

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Attentional bottlenecks force animals to deeply process only a selected fraction of sensory inputs. This motivates a unifying central-peripheral dichotomy (CPD), which separates multisensory processing into functionally defined central and peripheral senses. Peripheral senses (e.g., human audition and peripheral vision) select a fraction of the sensory inputs by orienting animals' attention; central senses (e.g., human foveal vision) allow animals to recognize the selected inputs. Originally used to understand human vision, CPD can be applied to multisensory processes across species. I first describe key characteristics of central and peripheral senses, such as the degree of top-down feedback and density of sensory receptors, and then show CPD as a framework to link ecological, behavioral, neurophysiological, and anatomical data and produce falsifiable predictions.

CPD: a unifying framework across species

All brains suffer a processing or attentional bottleneck because neural processing consumes a large fraction of available metabolic energy [1]. For example, each second human vision recognizes only about 40 bits out of 20 megabytes of input information into human eyes (roughly two short sentences out of a whole book of text) [2]. We are therefore blind to more than 99% of visual input information. This attentional bottleneck is shared across senses, such that being less blind to visual inputs causes more blindness in the other senses [3]. Organisms are therefore faced with a major challenge: they must process the most important features of their environment but cannot process all of the input information.

Two processes help organisms meet this challenge: **sensory selection** (see Glossary) and **sensory decoding**. During sensory selection, a tiny fraction of the sensory inputs available is selected for deeper processing inside the bottleneck. During sensory decoding, objects are inferred (i.e., perceived, recognized, or discriminated) from the selected inputs. Selection typically makes animals orient (e.g., by a gaze shift) to the selected inputs, centering the selected input within a special range of sensory locations (e.g., visual fovea) or feature values (e.g., of frequencies of echo sounds for bats). I refer to this special range as the **central sensory field** and the sensory locations or feature values outside this range as the **peripheral sensory field**. Sometimes I use the term fovea to refer to the central sensory field, borrowing the concept from retinal fovea. Prior to orienting, the inputs that will ultimately be selected typically fall in the peripheral field. Therefore, the peripheral field should be mainly concerned with selecting the target to which to orient.

Hence, I propose the CPD as a framework for studying multisensory processes across species (Figure 1A), extending the original CPD for human vision [4,5]. CPD defines peripheral and central senses functionally as those mainly engaged and specialized in selection and decoding, respectively. Accordingly, for each animal species, the identity of central and

Highlights

Only a fraction of sensory input is selected and recognized. In primate vision, selecting and recognizing are looking and seeing, specialities of peripheral and central vision.

In primates, feedforward inputs drive seeing both foveally and peripherally; feedback processes sculpt seeing foveally.

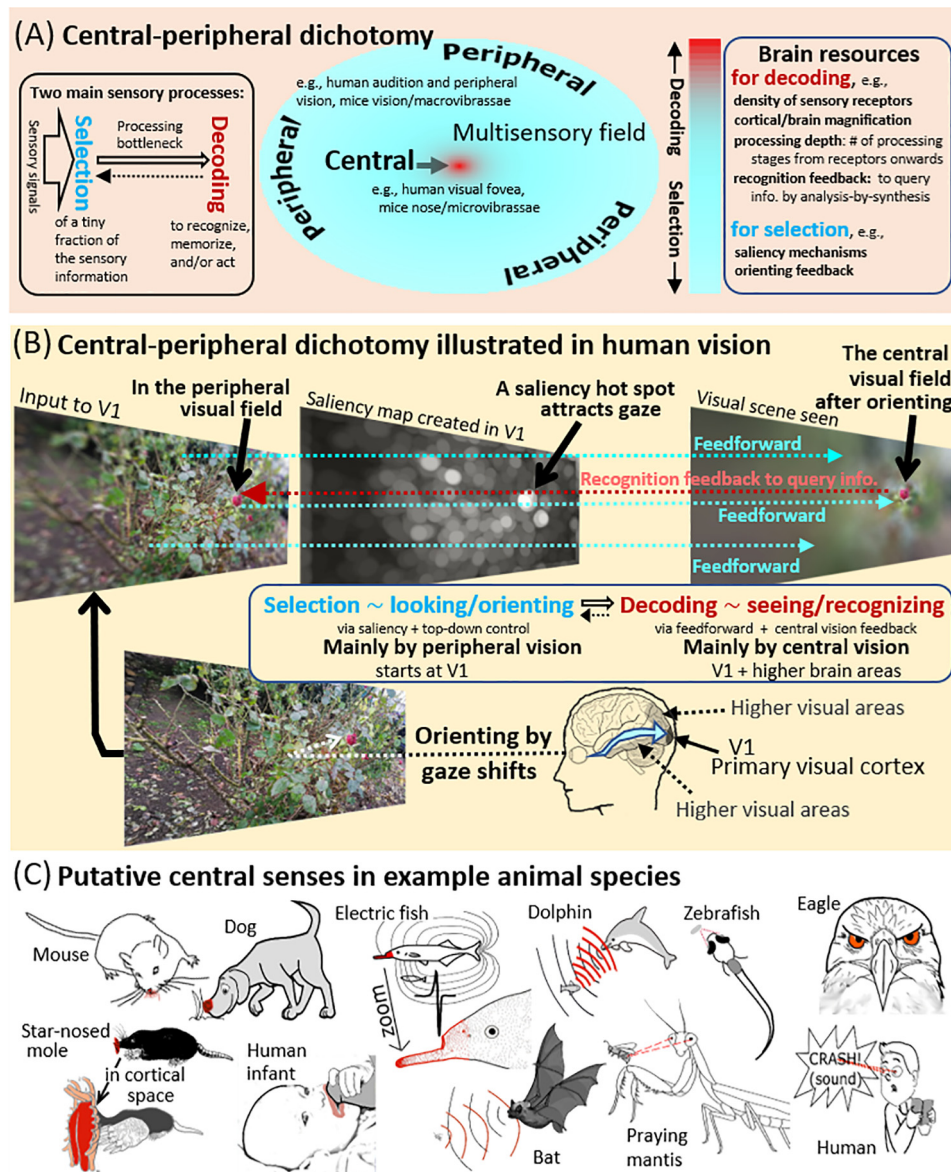Selection and recognition are extended across multiple senses.

Across animal species, selection can also involve orienting, for example, head, limb, whiskers, tentacles, snout, and/or ear, instead of gaze; central recognition can also involve, for example, microvibrissae (mice), nose (dogs, mice), lips and tongues (human infants), and/or acoustic fovea (bats).

Species with larger prefrontal cortices should have better endogenous control over orienting and feedback for recognition; these feedback controls facilitate decision-making for survival, learning, and creativity.

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Figure 1. Central-peripheral dichotomy (CPD) across senses and species. (A) The brain's processing bottleneck imposes selection and decoding as the two main sensory processes. CPD defines the peripheral and central sensory fields as the sensory locations or feature spaces mainly for selection and decoding, respectively. Decoding demands extra resources, including receptor density, cortical magnification, depth of processing hierarchy, and recognition feedback (to query more information by analysis-by-synthesis). Selection demands resources, for example, for saliency computation and top-down feedback control to orient attention. (B) In human vision, selection and decoding are mainly looking and seeing, executed by the peripheral and central visual fields, respectively. Looking orients the fovea to selected locations, guided by bottom-up saliency (computed in V1) and top-down goals. Accordingly, selection starts at V1, forwarding a tiny fraction of visual inputs through an attentional processing bottleneck. Decoding or seeing recognizes objects in the selected input; it is mainly performed by central vision, which is favored by top-down feedback to aid recognition. (C) CPD in example animal species. A red hue visualizes associations with putative central senses, which are nose and microvibrissae in rodents, tactile fovea in star-nosed moles, olfaction in dogs, oral tactile fovea in human infants, electrosensory fovea in elephantnose fish, auditory fovea in echolocating bats and dolphins, and binocular fovea in zebrafish, praying mantises, eagles, and humans. For each species, the other senses are putatively relatively peripheral (e.g., audition serves peripherally in humans to orient gaze).

Glossary

Analysis-by-synthesis: a method to analyze sensory input signals to recognize sensory objects/features. For each of multiple guesses (hypotheses) about the object identities/features of the sensory inputs, synthesize the would-be sensory input signals for this guess; assess the agreement between the would-be and actual signals for each guess; then pick the guess with the best agreement.

Central sensory field: a special range of sensory locations (e.g., human fovea) or feature values (e.g., sound frequencies) of highest sensory acuity, which are preferentially used to recognize selected (attended) sensory inputs.

Cortical/brain magnification: quantity of neural resources (e.g., cortical surface area, brain volume, neurons) per unit of sensory input space in, for example, visual image, skin surface, or frequencies of sound.

Feedback verification: during recognition, for a perceptual guess (hypothesis) about the sensory inputs, downstream stages along the sensory pathway (from receptors onwards) use analysis-by-synthesis to synthesize the would-be sensory input signals at an upstream stage; the would-be signals are fed back upstream to compare with the actual sensory input signals; the guess is verified or rejected by a good or poor agreement between the would-be and actual signals.

Feedforward-feedback-verify-reweight (FFVW): among perceptual guesses (hypotheses) fed forward by the sensory pathway about sensory inputs, the weight for each guess increases/decreases when the feedback verification of this guess succeeds/fails. Then, the highest weighted guess is selected as the recognition outcome.

Feedforward-weight (FfW): a method to recognize sensory objects/features using sensory signals fed forward along the sensory pathway. The feedforward signals can suggest multiple, individually weighted, guesses (hypotheses) about object identities/features; the perceived object identity/feature is the highest weighted guess.

Flip tilt illusion: a peripheral visual illusion in which the orientation of the displacement between two neighboring dots appears orthogonal to its actual orientation, when one dot each is black and white on a gray background.

peripheral senses can be inferred from behavior and brain organization (Table 1). For example, because humans orient mainly by gaze shifts, their central field is the central visual field and their peripheral field includes the peripheral visual field and sensory locations and features (e.g., sound frequencies) for other senses such as audition and touch. Human gaze shift to a sound source (Figure 1C) provides an example of selection by audition before decoding by central vision.

The central sensory fields at, for example, human visual fovea, mice microvibrissae (short whiskers closer to the nose, mouth, and chin), or optimal frequencies of echo sound for bats (Figure 1C), should thus have higher sensory acuities behaviorally. They should be prioritized for decoding resources, which can be (Figure 1A):

(i)   sampling density by the sensory receptors,
(ii) **cortical/brain magnification** by, for example, neural selectivities, area of cortical surfaces, and volumes of the brain regions devoted to one unit measure of the sensory field (e.g., visual field),
(iii) **processing depth** (i.e., the number of processing stages or levels from lower to higher processing stages along the sensory pathway),
(iv) **recognition feedback** to query more information to supplement the impoverished information let through the bottleneck, using an **analysis-by-synthesis** computation.

Conversely, resources devoted to the peripheral senses should be prioritized for orienting. Hence, they are characterized by:

(i)   sparser sensory receptors sufficient for detecting (rather than discriminating) objects,
(ii) **saliency** mechanisms to orient based on exogenous sensory input,
(iii) **orienting feedback**, if available, to orient based on top-down, endogenous, goals.

Importantly, central and peripheral senses are relative, constituting a continuum, rather than this simple binary caricature. For example, humans can decode or recognize objects in the peripheral visual field, just less well than in the fovea. There can also be multiple graded foveae in a single animal. For example, each retina in eagles and pigeons has a monocular fovea and a binocular fovea for lateral and frontal visual fields. The binocular fovea seems to be more central, since it has a higher behavioral acuity [6], and is the behaviorally preferred fovea for slower visual inputs at closer distances to intended prey or food [6–8].

Because CPD defines central versus peripheral senses according to their function of decoding versus selection, a sense that is central in typical situations can be peripheral in other situations. For example, although olfaction is typically central to mice, it could function peripherally to orient an animal by detecting distant objects. Similarly, in humans, lips, finger-tips, and nose are typically peripheral but can dominate decoding as central senses when visual information is unavailable or poorer (e.g., in infants before vision matures) [9,10] (Figure 1C). Hence, the putative central senses (listed in Table 1) are those that are typical or most common, but may not apply to all situations.

CPD provides a framework to link ecological, behavioral, neurophysiological, and anatomical data and makes novel predictions, particularly from orienting behavior to brain organization and vice versa (Table 1). In the coming sections, I first provide an example of this in humans with a focus on human vision before expanding across senses and animal species. I then examine evolutionary trends of decoding and selection.

Orienting feedback: feedback from downstream to upstream stages along the sensory pathway to aid attentional selection.
Peripheral sensory field: sensory locations or feature values outside the central sensory field.
Processing depth: the extent of signal processing by the brain (assessed approximately by the number of processing stages from sensory receptors onwards along the sensory pathway) to achieve an outcome.
Recognition feedback: feedback from downstream to upstream stages along the sensory pathway to aid recognition.
Saliency: the strength with which a sensory location attracts attentional selection (or orienting) solely by exogenous sensory inputs.
Sensory decoding: inferring sensory objects/features from selected (attended) sensory inputs. Also referred to as object recognition and discrimination.
Sensory selection: choosing a fraction of sensory input to pass the bottleneck restricting the brain's deeper processing, often by orienting sensory organ(s) of the highest acuity (e.g., gaze, nose, ears, or fingers) towards the selected input. This is often called attentional selection.

Table 1. Central-peripheral dichotomy in example animal species

Species	Putative central sense(s)	Indicative observations in behavior, neural selectivities, and neural anatomy	Predictions (confirmed[c] or to be tested)	Refs
Human/ monkey	Binocular visual fovea	Typically orient by saccades; vision typically dominates other senses in behavior; largest cortical area for vision among all senses; denser photoreceptors at fovea; larger V1 area per retinal ganglion cell at smaller eccentricities; V1 and V2 cover both the central binocular and the lateral monocular fields, whereas downstream higher visual cortices, for example, V4, in the ventral stream increasingly cover the more central, binocular, field only.	Flip tilt illusion[c] and reversed depth illusion[c] in peripheral vision; temporal and eccentricity dependence[c] of visual percept of reversed-feature signals	[2,21–23,31,56,86]
Raptor/ pigeon	Binocular visual fovea	Orient by gaze shifts; each retina has a monocular fovea at/near its center for lateral visual field and a more temporal binocular fovea for frontal visual field; higher acuity and greater sensitivity to slower moving inputs in binocular than monocular foveal region; denser photoreceptors and larger magnifications in optic tectum for both foveae; forebrain represents only the binocular fovea.	Across species of, for example, diurnal raptors, smaller lateral, monocular, visual fields correlate with better sound localization	[6,8,55,57,68]
Praying mantis	Binocular visual fovea	Higher behavioral acuity and sampling density at fovea; saccade to foveate on prey; stereo vision behaviorally; neurons tuned to binocular disparity.	Priority to central stereo vision in central brain	[46,53,87,88]
Zebrafish	Binocular visual fovea	Move eyes before moving head when orienting; two eyes follow inputs synchronously and converge on prey before capture; hydromechanical sense overshadowed by vision for rheotaxis; denser receptors at fovea; optic tectum prominent in brain.	Binocular disparity-tuned neurons; central brain's emphasis on binocular foveal region	[45,89–91]
Echolocating bats	Auditory fovea (sound frequencies of highest acuity)	Acoustic gaze control during prey approach in light or darkness; Doppler compensation of sound frequencies of calls during flight to foveate echo frequencies; foveal frequencies coded by higher magnification in cochlear, inferior colliculus, and auditory cortex, particularly for those most diagnostic of prey insects' wing flutter, movement directions, and identities.	Emphasis in neural tuning and brain volume for foveated echoes, for example, from buzz calls (with shorter inter-pulse intervals and, for bats, shorter pulses) in approach to prey	[40–43]
Dolphin (toothed whales)	Audition (sonar) for echolocation	Acoustic gaze control; object recognition typically better by echolocation than vision (or better by sampling the object first by sonar before subsequent matching by vision than the reverse); cortical and subcortical areas largest for audition among all senses.		[43,51,92]
Elephantnose fish	Electrosensory foveae for slower signals	The foveae, at chin appendage and nasal region, have denser receptors and higher magnification in electrosensory lobe; hypertrophied brain for electroreception; the chin appendage probes like a finger for object scrutiny; more discharge by electric organ for active sensing when swimming in direction to bring object closer to foveae.	Foveal signals more represented and processed in midbrain and forebrain (i.e., beyond hindbrain)	[37–39,50,93,94]

Table 1. (continued)

Species	Putative central sense(s)	Indicative observations in behavior, neural selectivities, and neural anatomy	Predictions (confirmed[c] or to be tested)	Refs
Human infants	Tactile oral fovea, perhaps also olfaction	Typically bring non-food objects of interest to mouth rather than eyes for scrutiny before vision matures (partly by increasing cone density in central retina); more likely than adults to orient their heads rather than gaze, presumably to orient their lips, tongue, and nose, to attended objects.	More (compared with adults) emphasis of oral tactile signals, perhaps also olfactory signals, in central brain	[9,10,36]
Star-nosed mole	Tactile fovea and olfaction	The tactile fovea contains the two lower-central appendages around mouth and nostrils; tactile fovea orients in a saccade-like manner during foraging; little brain response to visual inputs; foveal appendages and olfaction are over-represented in cortex.	Little top-down feedback to V1 for visual recognition	[33,49,95]
Dog	Olfaction	Apparent olfactory prevalence in behavior; across breeds, a weaker retinal foveal pit correlates with a more prominent nose, a larger fraction of brain for olfaction correlates with a smaller fraction for vision; the number of functional olfactory receptor genes for dogs is comparable with that for mice and about three times that for humans; compared with humans, dog's olfactory receptor neurons are many times more numerous, their odor detection sensitivity is 4–5 orders of magnitude higher; their olfactory regions connect extensively to other brain regions, including the occipital lobe.	Across breeds, a more prominent nose correlates with weaker recognition feedback to the central visual field in V1 from higher visual cortical areas	[48,96–99]
Rodents	Olfaction and somatosensation by microvibrissae (short whiskers closer to the nostrils, mouth, and chin)	In rats, touch dominates vision when the two senses conflict; mice rely on whiskers rather than vision, even for running at high speed amid obstacles; rodents preferentially use microvibrissae closer to their snout for recognizing objects and macrovibrissae for detecting and selecting objects; during prey capture, head movements (to orient nose and microvibrissae) typically lead or cause eye movements (in contrast to human behavior) to align gaze with head direction or via a vestibular-ocular reflex; no fovea in retina; narrow binocular field, has stereo vision but vergence does not adjust to object depth, neurons tuned to binocular disparity are less responsive to anticorrelated (than correlated) random-dot stereograms; larger cortical areas for olfaction and somatosensation than for vision.	The frontal binocular visual field is increasingly emphasized over the monocular visual fields for decoding in higher cortical areas and as the target of top-down feedback, despite its neglect by the center of each retina. Higher magnification in the brain for sensory inputs (per unit volume of peripersonal space) from microvibrissae than from macrovibrissae, especially for object discrimination (rather than navigation or orienting)	[32,47,60,61,100–106]

CPD interprets and predicts behavioral and neural data

CPD in humans and particularly in human vision

In humans and monkeys, orienting predominantly involves gaze shifts. Therefore, selection and decoding are 'looking' and 'seeing' [2] (Figure 1B). This is consistent with data [11] (Table 1). Hence, human CPD can be studied by examining central versus peripheral vision.

Box 1. V1 Saliency Hypothesis (V1SH) and saliency read out

A visual location's saliency is defined as its strength to attract attention or gaze exogenously. According to V1SH, saliency is signaled by the highest response from V1 neurons responding to this location [108]. For example, a uniquely left-tilted bar among right-tilted bars in Figure IA attracts attention automatically because it evokes a higher V1 response than any other bar. This higher response is due to a V1 property called iso-orientation suppression: neighboring V1 neurons (whose receptive fields cover nearby visual locations) suppress each other's activities; by iso-orientation suppression, this suppression is stronger when these neurons are tuned to the same or similar orientation. Hence, a neuron most activated by one background bar in Figure IA is under iso-orientation suppression from neurons most activated by nearby background bars, since these responding neurons are tuned to the common orientation shared by these background bars. Meanwhile, a V1 neuron tuned, and responding, to the uniquely tilted bar escapes this iso-orientation suppression. Thus, its response to this scene is the highest, making the uniquely tilted bar most salient.

Analogously, a uniquely red item among green items, or a uniquely leftward moving item among rightward moving items, attracts attention automatically because V1 has iso-color and iso-motion-direction suppression (see [2] for a pedagogical review). Since iso-eye-of-origin suppression is present in V1, V1SH predicts that an item with a unique eye-of-origin (Figure IB) is salient and attracts attention automatically. This is indeed confirmed, even when this eye-of-origin is invisible to seeing (because neural responses in higher brain areas do not depend on whether the left or right eye receives a visual inputs). This gaze capture by saliency can overwrite an endogenous control for a visual search task (Figure IB).

V1 saliency signals are monosynaptically projected to midbrain's superior colliculus, called optic tectum in non-mammals. In superior colliculus, superficial layers receive V1 and retinal signals; deeper layers receive inputs from the superficial layers, from endogenous guidance for attentional shifts, and from other senses, and project to brain stem to execute gaze shifts [17,18].
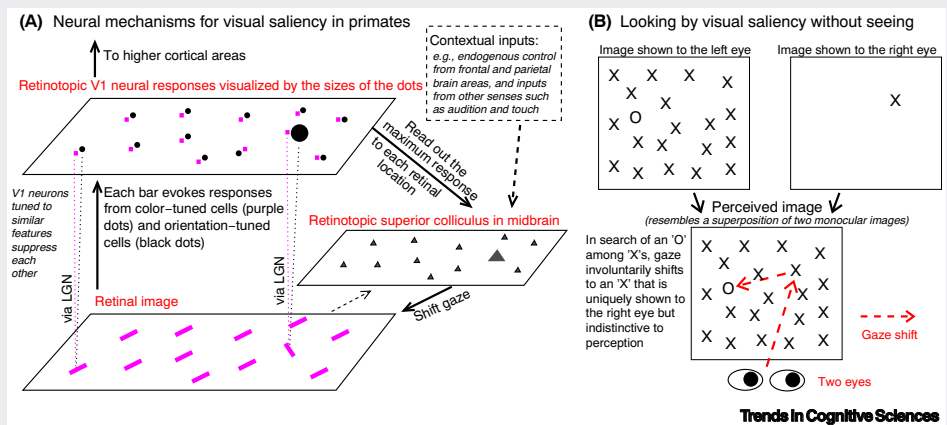

Figure I. Visual saliency in primates. Its neural mechanisms (A) and an example manifestation in behavior (B).
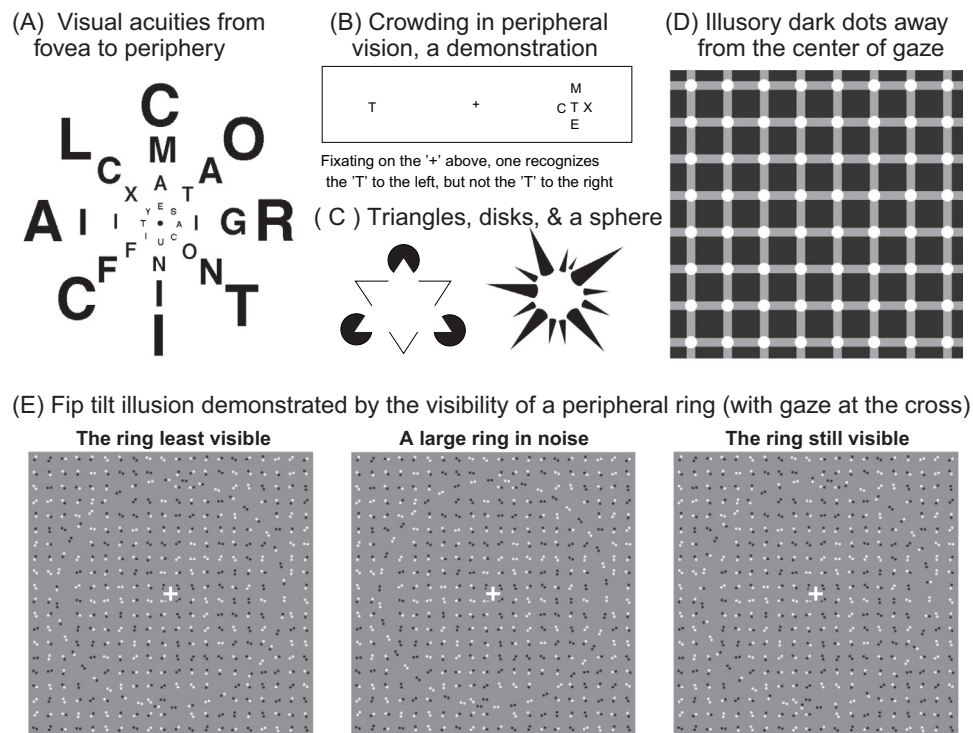
Where to look is controlled endogenously and exogenously. For example, endogenous goals might direct gaze to a book page, whereas a flying insect beyond the page might distract gaze involuntarily and exogenously. Traditional studies [12,13] have suggested that frontal and parietal brain areas, associated with intelligent control, guide both endogenous [14,15] and the exogenous [14,16] looking. More recently, the V1 Saliency Hypothesis (V1SH) has asserted that the primary visual cortex (V1) creates a saliency map of the visual field to guide gaze exogenously (Box 1). Exogenous saliency signals from V1 join endogenous selection signals from frontal and parietal brain regions to guide gaze via the subcortical superior colliculus [17,18]. V1SH is supported by, among others [2,19], the surprising demonstration (see Figure IB in Box 1) that looking can occur without seeing.

V1SH motivates the suggestion that the attentional bottleneck starts with V1's output [5] to downstream visual areas along the visual pathway, blocking (at least) information about the eye-of-origin of visual inputs (Box 1). Decoding must be understood in light of this bottleneck.

V1 could suggest multiple initial hypotheses (guesses) about the scene to higher brain areas downstream (e.g., the object at the center of gaze in Figure 1B could be an apple or a rose). Each hypothesis is weighted by evidence in the information-impoverished feedforward V1 signals.

Seeing could proceed downstream in two possible ways. One is to choose the highest weighted initial hypothesis (e.g., the rose), as the perceptual outcome. The other is to feedback to V1 (and/or other upstream regions) to query more information, thereby verifying and reweighting the hypotheses to make the perceptual decision. These two computational processes are called, respectively, **feedforward-weight (FfW)** and **feedforward-feedback-verify-reweight (FFVW)** [4]. Among the brain's decoding resources listed in Figure 1A, recognition feedback is present in FFVW but is absent in FfW.

According to the CPD for human vision, seeing in the central and peripheral visual fields mainly involves FFVW and FfW, respectively [4,5]. In FFVW, for each alternative hypothesis

(A) Visual acuities from fovea to periphery

(B) Crowding in peripheral vision, a demonstration

Fixating on the '+' above, one recognizes the 'T' to the left, but not the 'T' to the right

(C) Triangles, disks, & a sphere

(D) Illusory dark dots away from the center of gaze

(E) Fip tilt illusion demonstrated by the visibility of a peripheral ring (with gaze at the cross)

The ring least visible   A large ring in noise   The ring still visible

Figure 2. Manifestations of the central-peripheral dichotomy (CPD) in human vision. (A) Each letter is equally legible when one fixates (i.e., directs gaze at) the central dot, as visual acuity drops with eccentricity (the distance from a visual field location to the center of the visual field) [107]. (B) The two identical Ts are equally distant from the central cross; only the uncrowded T (left) is legible when one fixates the cross. (C) Triangles, disks, and a sphere are seen, despite patchiness in depictions. (D) A demonstration that peripheral vision is more vulnerable to visual illusions: dark dots appear only in the white disks away from the center of gaze. (E) A demonstration of the flip tilt illusion (in peripheral vision) predicted by CPD. Each image contains homo- and hetero-pairs of dots (two dots of the same and opposite contrast from the background, respectively). Dot-pairs in the background are randomly oriented. In the left/central images, all dot-pairs on a ring centered on the central cross are oriented along the ring, 50/0% of them are hetero-pairs. CPD predicts that hetero-pairs in peripheral vision will be illusorily perceived to have an orientation perpendicular to their actual orientation. This flip tilt illusion makes the ring harder to see in the left than the central image when one fixates the cross (placing the ring in the peripheral visual field). It also makes the ring easier to see in the right than the left image (fixating on the cross); note that the right image differs from the left one only in the orientations of the hetero-pairs on the ring (by 90°).

(e.g., 'apple'), higher areas use their internal model of the visual world to synthesize a would-be visual input that should agree with the upstream, actual, input if the hypothesis is correct. This would-be input is fed back and compared with the actual input in lower visual areas; the degree of match between the would-be and actual inputs is the queried information. A better match makes the hypothesis more likely to be the actual perceived object (i.e., the weight for this hypothesis for becoming the final percept is increased) [5,20]. This FFVW analyzes visual inputs by synthesizing inputs (analysis-by-synthesis). CPD predicts stronger recognition feedback in the central than peripheral sensory field. Human visual behavior supports this prediction [4,21–24].

FFVW enables our fovea to recognize the letter 'T' in Figure 2B regardless of whether 'T' is crowded by surrounding letters. This 'T' in the periphery is recognizable when uncrowded, suggesting sufficient retinal sampling resolution; but information loss after V1 makes it unrecognizable when crowded. Relying on FfW rather than FFVW, peripheral vision cannot resolve this ambiguity.

Without **feedback verification** vetoing misleading V1 signals, peripheral vision is also more vulnerable to illusions [5] (see example in Figure 2D). Illusory conjunctions (e.g., seeing a red-vertical line in an image of red-horizontal and green-vertical lines outside the attentional spotlight) [12] can be understood accordingly [5]. From this perspective, two new illusions are predicted and were subsequently confirmed: the **flip tilt illusion** [22] (Figure 2E) and the reversed depth illusion [21]. These are analogous to the reversed phi motion illusion [25] and can be understood as follows: a pair of two neighboring inputs (e.g., a homo-pair of two dots in Figure 2E) forms an orientation feature, to which V1 neurons are tuned. When a black dot pairs with a white dot [in a hetero-pair of dots (Figure 2E)], V1 neurons flip their preferred orientations by 90° [22,26,27,]. V1 feeds forward these flipped orientation signals, evoking the flip tilt illusion in peripheral vision where feedback verification is unavailable. Analogously, when a black dot in one eye pairs with a white dot in the other eye, V1 neurons' preferred depth (near or far) reverses; many such hetero-pairs can form a so-called anticorrelated random dot stereogram to evoke the reversed depth illusion [21]. In central vision equipped with FFVW, such illusions are weaker or absent.

Decoding may devalue unverifiable peripheral V1 signals in favor of extrapolations from verifiable central visual signals, as manifested in uniformity illusions [28]. Our impression of seeing our whole visual field clearly, despite inattentional blindness, is such an illusion.

When a sound source attracts gaze, audition joins peripheral vision to select sensory locations for foveal vision (Figure 1C). Indeed, auditory cortical signals project to V1 regions encoding the peripheral, but not central, visual field [29], likely influencing the saliency map in V1. Additionally, auditory and other sensory signals join visual signals in the superior colliculus (Box 1) to execute selection [18].

Central decoding can combine selected inputs from multiple senses (e.g., combining inputs from retinal fovea and finger-tips). Indeed, multisensory associative cortices and frontal regions downstream along sensory processing pathways project only, or more strongly, to central V1 [29,30]. These projections are consistent with the feedback-verify-reweight function in FFVW. For example, lip-reading can use such feedback verification to aid speech comprehension, and the McGurk effect arises when visual signals veto auditory ones (implicating the anterior cingulate cortex and inferior frontal gyrus [31]).

CPD across animal species

Orienting behavior in other animal species also enables their central sensors to sample and process selected inputs better, although data are typically less abundant. Table 1 lists putative central senses for certain animal species. Rodents orient head and whiskers, rather than gaze, to

sense attended objects by olfactory receptors and microvibrissae [32]. Dogs point their noses towards interesting objects. Star-nosed moles are almost blind; when they forage, touching a prey with any of the 22 appendages of their star triggers orientation of their two foveal appendages to sense prey before ingestion [33]. Underwater, the appendages hold exhaled and re-inhaled air bubbles over the nostrils (next to the foveal appendages) for active odor sampling [34,35]. Human infants make slower and less accurate saccades [36] than adults before their vision matures to overtake their lips and tongue as central senses. The electrosense of electric fish functions best at close distances (Figure 1C). They stereotypically swim backwards to bring objects, presumably first sensed by sparser electrosensors on their body, towards their electrosensory fovea [37,38] at their head region [39]. The auditory fovea of echolocating bats is specialized for a narrow range of frequencies of echo sound, which have the highest resolution behaviorally and neurally [40,41]. During flight, bats orient this fovea by adjusting the frequencies of their call sound [40,41], maintaining their head (thus ear) orientation [42], and adjusting their acoustic gaze (by adjusting intensity, pulse duration, and interval between pulses of their calls) towards a prey target [43]. Dolphins also adjust their acoustic gaze [43] during prey approach; whereas there is so far no evidence that they move their eyes to follow moving objects [44]. Humans, zebrafish, praying mantis, eagles, and pigeons all have binocular foveae: their binocularly coordinated gaze shifts [8,45,46] prevail when approaching food at short distances. Humans and zebrafish move their eyes before moving head/body towards objects [45], in contrast to mice [32] (mantis and raptors have limited or no eye-in-head mobility).

Consistent with these orienting behaviors and putative central sensors, brain organization in terms of receptor densities, cortical/brain magnification, processing depth, and recognition feedback can be understood or predicted using CPD, as outlined in Table 1. In rodents, the binocular visual field is narrow and is not covered by central retina [47], but is aligned with the sensory field of the central sensors (i.e., the nose and microvibrissae); hence, CPD predicts a greater decoding emphasis on binocular than monocular vision in higher cortical areas. The dog is the only animal species with known connections between olfactory centers and occipital lobes [48]. A predicted correlation across breeds, between a more prominent nose and a weaker top-down recognition feedback to central vision in V1, arises from: (i) the inverse correlation between nose prominence and the peakedness of photoreceptor density at fovea, and (ii) CPD's link between this peakedness and recognition feedback to central V1. In star-nosed moles, CPD predicts little recognition feedback to V1, since their near-blindness and near-absent brain responses to visual inputs [49] imply a near absence of feedforward visual signals that would warrant verification feedback. Human infants' behavioral oral fixation and sparser cones in the retinal fovea [10] predict a stronger emphasis in their central brain on lips and tongues relative to an adult preference for central vision and fingers. In electric fish, over-representation of the electric fovea in electroreceptors and hindbrain [37] is predicted to continue in midbrain and forebrain, perhaps by further magnification factors, especially considering that these fish have heavier brains (relative to their organs) than ecological control fish [50]. In echolocating bats and toothed whales, data about neural representation of foveated echoes are either scarce (in toothed whales) or focused mainly on simple sensory features, such as sound frequencies (bats) [41] or anatomy [51]. CPD predicts that more complex characteristics of foveated echos, such as those for buzz calls (with faster pulse rates and, for bats, shorter pulse durations) [43] during approach to prey, should also be over-represented in neural responses, particularly in the central brain.

Among the species in Table 1 with a binocular fovea and behavioral stereo vision, binocular disparity-tuned neurons have been found in primates [2], raptors [52], and praying mantis [53]; however, zebrafish research is yet to find binocular neurons beyond those tuned nonlinearly to conjunctions of inputs to both eyes [54]. In both raptors and primates, deeper forebrain regions

are devoted just to binocular vision [55,56], even though the midbrain in raptors over-represents both the binocular and monocular foveae [57]. Commonalities across species in behavior and neural representations allow CPD to predict: (i) binocular disparity-tuned neurons in zebrafish, and (ii) a relative emphasis on binocular over monocular vision in forebrain or central brain, also in zebrafish and praying mantis. Across bird species occupying similar ecological niches, smaller monocular fields devoted to attentional selection should correlate with a compensatory better sound source localization.

Evolutionary trends in depth of decoding and selection

Depth of decoding

Decoding becomes deeper at further downstream stages along the sensory pathway: from sensory receptors, to cortical/brain magnification at each stage along the pathway, to recognition feedback from higher/deeper to lower/shallower decoding stages. CPD predicts an emphasis on the central sensory field at each decoding depth, particularly in deeper stages. This is exemplified by the over-representation of binocular, compared with monocular, signals in the forebrain of birds [55] and primates [2,4,56]. However, in simpler brains, decoding hierarchies can be shallower and recognition feedback may be largely absent. Among species with recognition feedback, CPD predicts stronger feedback to the central than peripheral sensory field. Through evolution, the forebrain and frontal cortex occupy larger fractions of the whole brain and cortex, respectively [58,59]. This predicts deeper decoding in higher animals. Compared with humans, rodents, for example, rely less on cortical (rather than subcortical) areas for, for example, somatosensation [60,61] and vision [62].

The deepest visual processing in praying mantis, which strikes at prey in its binocular strike zone [53], might not be deeper than that in V1 of primates. Primate V1 also has binocular cells and V1 activities can evoke saccades [19,63], which are motor responses like mantis strikes. Visual recognition feedback in primates, neurally (from higher to lower cortical areas) and behaviorally [4,23,64–66], may not be available in praying mantis. In praying mantis, feedback connections from central brain to lower visual stages have been observed [67]. However, they appear not to be the recognition feedback to verify whether the feedforward inputs make sense: mantis strikes at its 3D strike zone even if the zone contains only a virtual prey made by, for example, binocularly uncorrelated flickering dots at the corresponding locations in the two monocular images [53]. Future studies can test CPD by examining whether this observed feedback is for recognition or orienting feedback, or perhaps for other computations, such as gain control of neural responses and arousal.

Compared with humans, raptorial birds have higher visual acuity and photoreceptor density, but have fewer retinal ganglion cells per photoreceptor in the fovea [68]. Hence, their higher acuity is largely due to denser receptor sampling rather than deeper decoding. Like human central vision [21], owls have stereo vision and are not fooled by anticorrelated random dot stereograms [69]. Their disparity-tuned neurons in the forebrain have longer response latencies when they are more suppressed by such stereograms [69], suggesting a presence of the recognition feedback. For owls, CPD thus predicts stronger recognition feedback to the central binocular visual field. Apparently, among humans, birds, and praying mantis, visual decoding is deepest in humans and shallowest in mantis.

Through analysis-by-synthesis, recognition feedback in FFVW endows humans with visual understanding. Without this, contemporary artificial (feedforward) neural networks (ANNs) are (like human peripheral vision) easily fooled by adversarial attacks [70]. With such feedback, human central vision can imagine inputs in hypothetical scenarios, thus constructively complete, correct, or explain away visual inputs. Such feedback facilitates recognition when inputs are too challenging for ANNs due to object occlusion, clutter, or noise. With challenging inputs, primate neurons in higher visual cortical areas take longer to signal correctly for visual objects [64–66], consistent

with extra time needed for the feedback, which appears to involve ventrolateral prefrontal cortex [71]. Feedback in central vision vetoes the reversed depth illusion of a surface by an anticorrelated random-dot stereogram presented alone, but it allows this illusory depth to augment the perception of a non-illusory depth of another surface at the same location (by a concurrent, correlated, random-dot stereogram) when the two surfaces evoke responses from V1 neurons tuned to the same depth [23]. Such selective constructiveness in the feedback likely underpins our vivid perception of triangles, disks, and a sphere in Figure 2C from mere allusions and fragments. Lower animals have smaller or no prefrontal cortices for the recognition feedback. It is possible, therefore, that they have weaker imaginative perceptual power [72,73], such that in Figure 2C they might perceive the triangles [73,74] but not the sphere.

Depth of selection control

A larger forebrain and/or frontal lobe should also enable more orienting feedback (Figure 1A,B). In primates, this feedback is from the frontal eye field in the frontal lobe and from parietal cortex [14,18]. It converges with exogenous saliency signals from V1 at deeper layers of superior colliculus [17,18,62] (see Figure IA in Box 1) to enable voluntary selection. In lower animals, the forebrain control network is less elaborate [18], making behavior more easily predictable from (and distracted by) salient sensory drives. As humans age, frontal brain areas, but not V1, are reduced in size [75]. A relatively stronger exogenous control of orienting in older humans [76] could cause aimless wandering in the cognitively challenged older humans, as has been reported [77].

CPD predicts that among species with top-down orienting feedback, this feedback is mainly for peripheral senses (Figure 1A). In primates, along the visual pathway from V1, dorsal and ventral streams are associated with 'where'/'how' and 'what' vision and are thus for selection and decoding, respectively [2]. Therefore, CPD predicts that, for primates, orienting and recognition feedback, respectively, stemming from dorsal and ventral streams, preferentially target peripheral and central visual fields in lower cortical areas such as V1.

Selection and decoding for decision-making and learning

Both selection and decoding are forms of decision-making. Survival depends on good decisions concerning whether to orient to, for example, the left, the right, or to a particular object, and about whether the object is, for example, prey or predator. Indeed, humans and monkeys prefer looking towards objects associated with past rewards [78,79]. Through reinforcement, animals learn to make good decisions from sensory inputs about their environment, including about predicted consequences of their and other animals' actions [80]. Novel objects and events attract attention to help animals learn their associated reward values [81].

Decision-making, especially for voluntary decisions, relies heavily on forebrain and frontal regions. After learning object-reward associations, animals should learn to orient quickly to the most rewarding objects in future encounters when objects will typically be sensed initially by the peripheral sensory field. Monkeys, once familiar with the object-reward associations, become increasingly good with experience at aiming their first saccade to the more rewarding object in their peripheral visual field within 150 ms of object appearance [81] before prefrontal brain areas could register the rewards [82]. This behavior demonstrates the orienting role of peripheral senses according to CPD. It may arise from covert evaluations of the rewards [81], or may be another example of looking before seeing (see Figure IB in Box 1). Practicing is known to make visual orienting to rewarding objects increasingly reflexive via exogenous control by lower brain areas such as V1, superior colliculus, and basal ganglia [19,27,79,83]. This migration to lower level control of orienting is consistent with continued attentional capture by objects after they cease to be rewarding [78]; monkey V1 neural responses are modulated by reward knowledge with a latency

of 120 ms [84]. (For brevity, this paper does not discuss sensory inputs that require immediate escaping, avoiding, and coping actions rather than, or in addition to, orienting for decoding; such inputs can arise from, for example, looming predators, approaching projectiles, and navigational hazards, and typically appear first in peripheral sensory fields [85].)

When equipped with recognition feedback, the brain could use synthesis mechanisms to simulate scenarios and predict, for example, consequences of actions. This helps planning and imagination. Larger prefrontal cortices enable better and stronger top-down feedback for both orienting and recognition via a richer brain network for decision-making, planning, learning, and innovation.

Concluding remarks

Motivated by the ubiquitous attentional bottleneck, CPD defines central and peripheral senses by their decoding and selection functions. It provides links between sensory ecology, animal behavior, neurophysiology, and brain anatomy. It also provides a unifying framework to examine seemingly unrelated species through their shared central senses, shared computational dichotomy, and contrasting depths of sensory processing. It enables us to make predictions from orienting behavior to brain organization (and vice versa), to appreciate why raptors have higher visual acuity but shallower processing depth than humans; why human infants use their mouth, but adults use gaze, to scrutinize objects; and to discover common computational algorithms despite differences between gaze, nose, snout, tentacles, fingers, ears, and/or whiskers for scrutinizing objects. Future research can test the predictions in Table 1, make further progress by generating new predictions from CPD, and answer additional questions (see Outstanding questions) opened up by this framework.

Declaration of interests

No interests are declared.

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Outstanding questions

How do brains compute initial hypotheses about the visual scene from the initial feedforward V1 signals?

Do some variations of human visual capabilities, including deficits (such as dyslexia and prosopagnosia) and super-normal abilities (such as those of super-face-recognizers), arise largely from individual differences in their feedback and verification components in the FFVW process in central vision? For example, do human super-face-recognizers have a better internal model for synthesizing would-be visual inputs for faces?

Among animal species, is the human brain special as an extreme outlier in processing depth and feedback capacity, particularly in its ability for analysis-by-synthesis to imagine and simulate sensory and even abstract scenarios? Such top-down simulations can be very useful for, for example, visualization, metaphorical thinking, and language.

How can we quantify central versus peripheral processing to, for example, better justify or falsify the idea that dogs have olfaction as their central sense? One possibility is to measure respective brain volumes (e.g., cortical magnification factors) and/or sensors for one versus another sense, or one part versus another part of the same sense. Another is to segment sensory behavior into selecting and recognizing episodes in a way that is operationally feasible and computationally consistent across species and senses.

Analysis-by-synthesis is a computational algorithm for the recognition feedback; what is the computational algorithm for the orienting feedback?

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