Attention or salience?

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Abstract

While attention is widely recognised as central to perception, the term is often used to mean very different things. Prominent theories of attention – notably the premotor theory – relate it to planned or executed eye movements. This contrasts with the notion of attention as a gain control process that weights the information carried by different sensory channels. We draw upon recent advances in theoretical neurobiology to argue for a distinction between attentional gain mechanisms and salience attribution. The former depends upon estimating the precision of sensory data, while the latter is a consequence of the need to actively engage with the sensorium. Having established this distinction, we consider the intimate relationship between attention and salience.

Keywords: Attention; Salience; Bayesian; Active inference; Precision; Active vision

Introduction

Optimal interaction with the world around us requires that we attend to those sources of information that help us form accurate beliefs about states of affairs in the world (and our body). This statement may be interpreted in two very different ways. The first interpretation is that we (covertly) select from multiple sensory channels (either within or between modalities) and ascribe greater weight to those sensory streams that convey the most reliable information about states of the world [1]. The second interpretation calls for a more enactive approach [2]. It requires that we actively manipulate our sensory epithelia to (overtly) select the data we sense [3,4]. In this review, we argue that these interpretations – while equally valid – reflect distinct computational processes, mediated by different neurobiological structures [5].

A key concept in understanding the difference between the covert and overt sampling of our sensorium is a generative (predictive) model. Recent theoretical work calls on the idea that the brain possesses an internal model that tries to account for how sensations are generated by the external world [6,7]. Under this view, perception is a process of optimising beliefs about the causes of

sensations, while actions select new sensory data to test hypotheses about these causes [8]. While the notion of perception as hypothesis testing has a rich history [9,10], it is only recently that these ideas have been formalised in terms of the (active) inferential processes they mandate [11]. Anatomical pathways hint at the form of the generative model entailed by the brain. Connections from visual cortex to the dorsal ('where') and ventral ('what') streams (Figure 1) can be thought of as carrying evidence in favour of spatial configurations or stimulus identities, respectively [12]. Those from frontal areas to posterior cortices may signal predictions about the 'what' and 'where' information that would be obtained as a consequence of action (e.g. a saccadic eye movement) [13]. Alternatively, they may modulate the gain of signals in these pathways [14].

In the following, we first review recent work on attention as a process of gain control. This rests upon estimating how informative a particular kind of data is about a given hypothesis. We then move to a discussion of active vision, emphasising the role of saccadic eye movements in the performance of perceptual experiments. Finally, we attempt to reconcile these accounts of attentional processing, noting that unambiguous sensory data should be amplified when present, and should be sought when absent.
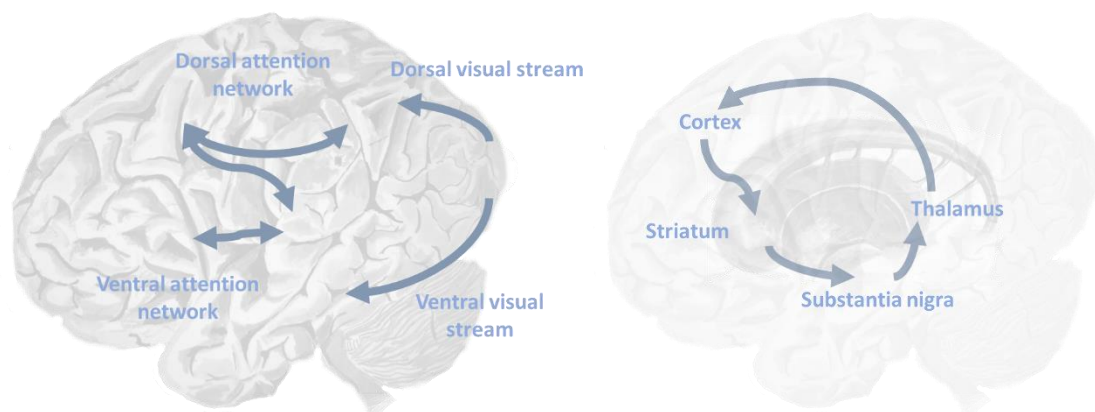

Figure 1 – The cortical and subcortical anatomy of attention The deployment of attentional gain selectively emphasises forward connections, such as those depicted in the cortical visual streams on the left. The beliefs[1] derived from these inferences can then be used to plan the next move, with competing plans evaluated in cortico-subcortical loops shown on the right. This implies a role for the basal ganglia in computing the salience associated with a given perceptual experiment (e.g., a saccade). Such computations rely upon beliefs about the mappings from controllable states (e.g., fixations) to their sensory consequences. These neuronal inferences manifest in the connections from dorsal frontal regions (the frontal eye fields) to dorsal and ventral regions in the posterior cortices that carry visual information about space and identity respectively.

Attention as gain control

Generative models are used to predict, based upon plausible hypotheses about the world, the sort of data that we will encounter. These data can then be used as evidence to confirm or refute these

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[1] In this article, beliefs referred to (posterior) probability distributions also known as pacing beliefs. These are not propositional or subjective beliefs and are generally considered subpersonal.

hypotheses. From a Bayesian perspective, the degree to which we should update our beliefs about the causes of a sensation depends upon the precision (inverse covariance) of the probabilistic mapping between the two (c.f. Kalman filtering). In other words, precision corresponds to the confidence afforded sensory evidence, given our knowledge about how it was generated. For example, if we hypothesise that visual impressions are caused by the capital letter 'A', there is a precise mapping from this cause to the visual form and shape. Sensations inconsistent with this shape represent evidence against this hypothesis. In contrast, there is an imprecise mapping from 'A' to visual wavelength information as the letter could be rendered in any colour. To disambiguate between the letters 'A' and 'B', we should attend to channels offering shape information, and away from those associated with colour. This simple example serves to illustrate the importance of precision in weighting different sorts of sensory evidence. Crucially, this generalises into the visuospatial domain, as the sensory data that can be solicited from different locations may be generated with differing levels of precision.

The above makes the intuitive case for the need to modulate sensory channels for perceptual inference. Doing so is important in selecting the right sensations to inform inference, but also in balancing internally generated (predictive) content with sensory evidence. This has been formalised in computational accounts of brain function [1,15-17], that implement attention through a multiplicative gain on ascending ('bottom-up') connections [18]. These theoretical treatments reproduce classical attentional phenomena; including the effects of cueing on reaction time in the Posner paradigm [1]. Similarly, figure-ground segregation, where a stimulus is distinguished from its background only by its second order statistics – like precision – can only be performed if precision can be estimated and used to contextualise visual data [19]. This perspective can be applied to a range of voluntary [20] and automatic [21,22] attentional phenomena.

Neurobiologically, this form of attention is thought to depend on synaptic modulation [23]. Acetylcholine has been repeatedly implicated in gain control in the visual cortex, where it increases the amplitude of cortical responses to visual stimuli [24,25]. This observation is corroborated by pathologies of cholinergic transmission, including Lewy Body Dementia [26], and their associated (hallucinatory) visual disturbances [27]. A deficit in estimating precision has been demonstrated in related disorders [28] and a role for acetylcholine in signalling sensory precision has been made explicit in theoretical accounts [29,30], and in empirical studies that estimate this quantity under pharmacological manipulations [31]. Cholinergic modulation represents one of many (possibly interrelated) mechanisms likely to underwrite precision optimisation; see [32-36].

Active perception and salience

In the previous section, we described the deployment of attentional gain to select informative sensory data. We now turn to a different form of selection that involves actively seeking new sensations. This allows us to actively construct our percepts [37-39] and underwrites formulations of visuospatial attention in terms of planned (covert) or executed (overt) eye movements [40]. This terminology derives from the premotor theory of attention [41]. The premotor theory draws evidence from behavioural studies – in which the deployment of covert attention alters saccadic trajectories [42,43] – and from the anatomy and physiology of the structures involved in attentional control. Specifically, there appears to be a substantial overlap between attentional and oculomotor

networks [44-48]. For the purposes of this paper, we group visuospatial covert attention (in which no eye-movement takes place) with the covert attentional processes considered in the previous section.

Formal accounts of attentional salience attempt to quantify the degree to which beliefs may be altered by the performance of a saccade to a given location. Intuitively, if the sensory consequences of an action are known before that action is performed, nothing new is learned by the performance of that action. Similarly, if sensory data are of a very low quality (i.e. are highly ambiguous), there is no point in sampling them. Salient actions are those that solicit unambiguous data that could not have been predicted with a high degree of certainty prior to that action. Salience has been defined (equivalently) in terms of intrinsic motivation [49,50], Bayesian surprise [51], a relative entropy [3], and a component of an expected free energy functional [37], where it is referred to as intrinsic or epistemic value. Interestingly, these have the same form as objective functions used to score experimental design [52] – endorsing the metaphor of 'the brain as a scientist'. In brief, the best (most salient) experiments are those that bring about the greatest change in beliefs. As such, there must be a relatively high degree of uncertainty about the data that will be acquired, but a high level of confidence in the way in which these data are generated. The latter ensures that sensations are informative about their causes, while the former is responsible for the phenomenon of 'inhibition of return' [53] that prevents repeated sampling of the same data. Put simply, salience scores the information gain or reduction in uncertainty "if I looked over there". After actually looking 'over there' I then become more confident about the causes of my sensations. Furthermore, having sampled a particular location, there is little epistemic value in looking there again. This is because the sensory data have already resolved uncertainty about the visual scene – and have nothing more to offer in terms of belief updating.

Figure 1 illustrates some of the key anatomical connections implicated in attentional and oculomotor systems. These include the dorsal and ventral frontoparietal networks and pathways from the cortex through the basal ganglia. Notably, lesions to each [54,55] have been reported to cause visual neglect – a common disorder of visuospatial attention in which patients fail to attend to the left side of space. This suggests that neglect is a disorder of salience attribution, consistent with the abnormalities of saccadic sampling observed in these patients [56]. Right hemispheric lesions that disconnect the dorsal from the ventral attention network might disrupt the connections that map contralateral fixation locations to their visual consequences [57]. This renders saccades to the left of space poor experiments; as visual data garnered from these can no longer elicit a change in beliefs. The basal ganglia have been implicated in evaluating alternative courses of action [58] – including as saccades to different locations. Under this view, neglect resulting from striatal lesions reflects a disruption of salience computations, while cortical disconnections disrupt the substrates of these computations.

Attention and salience

Although we have argued for a distinction between attention (as a process of gain control) and salience, it is possible to reconcile the two. Both represent beliefs about the capacity of sensory data to adjudicate among competing hypotheses. The former relies upon currently available data, while the latter depends on data that has yet to be acquired. An interesting consequence of this is a phenomenon sometimes called the 'streetlight effect' [59]. This is often portrayed as an unhelpful cognitive bias – and conjures the image of a drunkard who looks for his lost keys underneath the streetlight, as it is the only place he can see. There is a sense in which this is optimal behaviour, as

the unambiguous (precise) visual data obtained under the light supports stronger inferences than the darkness around it [30]. This example discloses a fundamental link between attention and salience. Those locations that afford unambiguous sensations should be afforded a greater attentional gain if within the visual field, while saccades that bring such locations within the fovea are highly salient.

Recent ideas about the nature of motor control illuminate another plausible interaction between salience and attentional gain. These advances suggest that commands are actually predictions that are enacted by spinal or brainstem reflexes [60]. As the fovea carries the highest density of photoreceptors in the retina, a prediction (i.e., motor command or setpoint for oculomotor reflexes) that a location in visual space will be foveated entails a belief that the precision associated with this location is high. The resulting saccade fulfils this prediction. This idea is consistent with observations concerning electrical stimulation of frontal neurons that induces saccades to a given location. Subthreshold stimulation of the same neurons increases the gain of neurons with receptive fields at that location [61], exactly as if the precision had increased. That these two mechanisms are so closely linked endorses the premotor theory of attention. This is because, in the spatial domain, deployment of covert attention (precision) to a given location biases planning in favour of an overt saccade to that (salient) location.

Conclusion

Attentional processes select those sensations that are informative about their causes. Broadly, these processes can be separated into two categories – those that optimise the weighting of current data, and those that mediate the acquisition of new sensations. While the former makes use of sensory data in the present, the latter is concerned with the future. Biologically, attentional gain reflects a modulation of synapses such that one type of sensory data is emphasised. This implicates ascending neuromodulatory systems and other forms of gain control [32,33], but may be contextualised by signals from other cortical and subcortical regions. Salience computations instead implicate connections between those areas that represent controllable states – e.g. fixation location – and their sensory consequences. The salience associated with a saccade to a given location may then be evaluated in cortico-subcortical loops. Although salience and gain control depend heavily upon one another, we argue that they are best understood as distinct perceptual operations that, when compromised, give rise to different neurological syndromes.

In summary, gain control is crucial in balancing influences on perception from competing sensory evidence and from internally generated prior beliefs. Failures to do so lead to false percepts, including hallucinations. In contrast, salience is afforded to actions that represent good perceptual experiments. Syndromes of aberrant salience computation manifest as failures of active scene construction.

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