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Modality general and modality specific coding of hedonic valence

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Abstract

The pleasant or unpleasant qualities that attach to our perceptions help to determine whether we approach or avoid environmental stimuli, shaping their affordances. How do brains create this affective perceptual dimension? The traditional answer is that sensory areas serve only as conduits for external impressions that are then modulated by heteromodal limbic structures in subsequent phases. Here we raise the possibility that, in addition to these well established gain control effects, sensory systems might also have a more direct role in representing the pleasantness component of perception, as supported by several strands of recent brain imaging evidence. In conjunction with a shared valence code that is independent of its sensory origins, valence representations interleaved within sensory brain areas may support finer grained experiential distinctions between how things look, sound, feel, taste and smell good or bad to us, offering a higher dimensional space of evaluative discriminations.

Introduction

In modular, cognitivist architectures of the mind, perception is segregated from affect, cognition and action, serving as the entry portal for impressions from the outside world [1]. Yet in natural settings animals do not wait to be activated by external stimuli — they spontaneously explore their surroundings, energized by expectations that are continuously updated through brain–body–environment interactions [2–6]. Sensory inflows, rather than mediating a passive transfer of information from the exterior world, function largely to constrain endogenous brain activities with the aim of satisfying the mandates of survival and reproduction [3,5]. External stimuli are simultaneously integrated with the organism's learning history and current physiological state, enabling sensory networks to rapidly extract the meaning and behavioral significance of environmental signals [6–8]. In this dynamicist model there is no 'pure' perception stage that precedes the affective consequences of selecting particular actions [3,9•].

The chief constraints operating on action-perception loops are those pertaining to primordial computations of good and bad (hedonic valence) [3,9•,10]. A number of models have been advanced as mechanistic accounts of how affectively salient stimuli amplify perceptual, attentional and mnemonic processes [11–14]. Inherent to these models is the concept that the affective qualities of stimuli modify perceptual function via re-entrant projections from heteromodal cortico-limbic structures. Sensory systems themselves have not been classically implicated as constituting components of hedonics beyond their role as mere conduits for exteroceptive inputs that are subject to gain control effects in a separate step. The representational space of the visual system, for instance, remains confined to the coordinate space of canonical physical features like orientation, contrast and spatial frequencies [15]. Here, we consider a complementary, and more radical possibility that elementary attributes of hedonic valence are also partially embedded within sensory areas alongside physical stimulus features [16]. With several exceptions [9•,17•, 18, 19], this concept is presently not widely entertained in the affective sciences.

Modality general coding of valence

Researchers have long assumed the existence of a single supramodal hedonic system that allows you to experience your cup of espresso, the smell of freshly cut grass and a gentle caress as pleasurable, each in its own right [20,21]. A common pleasure currency permits comparing discrepant forms of stimulation and the selection of appropriate courses of action [22,23]. Our recent findings from representational similarity analysis (RSA) (see Figure 1) indicate that in lieu of regional specificity for negative and positive valence, the representational geometry of activity patterns in the ventromedial and orbitofrontal cortices (OFC) supports affective discriminations across modalities, as indicated by the leaning of a population vector [17•]. This population vector is analogous to a kind of valence meter. Here, we advance a framework under which modality general valence meters are accompanied by various differentiated ones, partially residing within sensory brain areas.

Modality specific coding of valence

Perceptual systems are conventionally modeled as a hierarchical bank of low-level analyzers that encode and relay — in a bottom-up fashion — the physical dimensions of stimuli. Much of the work that fostered traditional theories was based on recordings from anesthetized rather than freely behaving animals [6,24]. Recent discoveries have established that even the primary sensory zones in many mammalian brains have the capacity for storing mnemonic residues of experiences related to reward and punishment [25, 26, 27•] and the anticipation of reinforcement [28,29•]. From this perspective, a major role of sensory networks is not to reflect object physics but rather to capture the significance of cues within a behavioral economy shaped by homeostatic demands [3,9•]. Below, we offer an abbreviated overview of select human studies that provide support for our hypothesis for the existence of modality specific representations of hedonic valence.

Olfaction

The human olfactory nasal epithelium is the receptive surface where odorants initially bind to their receptors. Advantageously for researchers, it is possible to use electro-olfactograms

to obtain direct recordings from the epithelial surface of humans while simultaneously measuring perceptual qualities of odors. Mapping neural activity to perception has revealed that the olfactory epithelium exhibits a patchy organization with a valenced tuning profile – recording sites with large responses to pleasant odors evinced similar response properties for other pleasant odorants and diminished responding to unpleasant ones [30]. An opposite profile (i.e. preferential responses to unpleasant odors) was discovered from recording sites in different patches. Some evidence supports the possibility that pleasant and aversive odor qualities are reflected in the physicochemical structure of the odorants themselves [31–33] and that these relations are conserved across species [34].

Gustation

On the basis of the findings in nonhuman primates that satiety fails to modulate activity recorded from the primary taste cortex (frontal operculum and insula), it was suggested that these regions code only for objective gustatory properties, such as tastant concentration [35,36]. However, the evidence is somewhat more mixed [37] when considering results from human neuroimaging studies (reviewed in [38]). One study reported expectancy-driven modulation of the human mid-insular cortex and operculum, such that bitter tastes evoked less activity when subjects were led to believe that ingested solutions would be less aversive [39]. This finding is consistent with reports that electrical stimulation of the anterior and mid-insular cortex of humans can elicit unpleasant taste sensations [40]. Recently, we have used multivariate pattern analyses to demonstrate that independently of basic taste type (bitter, sour, etc.), gustatory valence is encoded in response patterns within the anteroventral insula and posterior orbitofrontal cortex (OFC), putative primary and secondary regions of human gustatory cortex [17•]. Critically, these patterns for gustatory valence were not shared with those encoding visual valence. It should be noted that the boundaries of human primary taste cortex are disputed and there is evidence to suggest that the anterior insula and OFC constitute multimodal limbic cortex, rather than gustatory cortex *per se* [41]. As noted earlier, response modulation as a function of expectations concerning gustatory valence also appears to extend to more posterior (sensory) portions of the insula [39].

Touch

In the somatosensory system, C fiber afferents, acting via slow unmyelinated pathways, mediate the aversive or pleasurable components of touch [42]. Since the terminal pathways of pain and pleasure C-fiber afferents project heavily to limbic zones [42], affective touch has been viewed as processed by regions such as the insula, OFC and anterior cingulate, while primary somatosensory cortex activity is predominantly responsive to the discriminatory (non-affective) aspects of cutaneous stimulation [43]. However, in an intriguing set of findings, differential effects of reward were observed in human primary somatosensory cortex (SI) in the absence of actual stimulation – and these effects scaled with reward magnitude ([44], see [45, 46] for similar findings in V1). In another study, activity in SI was modulated by the pleasantness of a social caress independently of sensory stimulation, suggesting a direct role for this region in valence discrimination [47].

Vision and audition

Several recently published reports have set out to use multivariate pattern analyses to recover modality general and modality specific valence representations of visual and auditory affective cues [48•,49]. Providing direct support for our central hypothesis, Shinkareva and colleagues [48•] found that visual and sound specific valence could be successfully decoded, even when based solely on information from the respective primary sensory cortices. The visual and auditory representations of valence were orthogonal across modalities. A meta-analysis of several hundred human brain imaging studies concluded that activity in the early sensory regions of all modalities is involved in constructing modality-specific affective experiences [19].

To further probe how and where the human brain represents stimulus features alongside their pleasantness, we [17•] exposed participants to visual scenes and tastants continuously ranging in valence. Each experimental trial was modeled as a discrete event and used in an RSA analysis to reveal how the geometry of population level activity corresponded to similarity–dissimilarity in objective stimulus properties and subjective valence experiences. Not surprisingly, this analysis revealed that response patterns in the early visual cortices were most reliably organized by gradations of low-level features like contrast and luminance. Alongside these sensory properties, population coding of self-reported hedonics was reflected in distributed swaths of cortex. Multivoxel patterns of activity in the ventral stream were diagnostic of hedonic valence specific to the visual modality, not shared with gustatory pleasures of ingested liquids (Figure 1d). The representational geometry of this code reflected experienced valence distance, with trials of similar valence (e.g. puppies and a sunset) located in a similar part of this neural representational space while trials with opposing valence (e.g. puppies and feces) were most distant. Brain responses were not merely expressing gain modulation of co-localized stimulus features, since they were distinct from low-level physical or associated high-level object properties (e.g. animacy) of the images. The continuous nature of valence experience, although not a dimension of the physical world like luminance, was mirrored within regions of the brain where topographic fidelity breaks down into modality specific higher order representations.

A functional role for modality-specific affect codes

Why might the brain maintain diverse representational codes for hedonic valence, some of which are supramodal while others are bound to specific modalities and what is their potential relevance for behavior? One possibility is that modality specific valence codes are advantageous for passing on weighted features that are integrated into a multifaceted index of value by heteromodal brain structures (see Figure 2). While cross-modal hedonic interactions are often synergistic [50,51], this may not always be the case. A common hedonic valence code necessitates dimensionality reduction. However, situations that involve competing environmental affordances may benefit from higher-dimensional valence discriminations. A food that is visually repulsive (e.g. slimy, green meat) is very likely to be avoided no matter how pleasant its aroma or taste. The distinct ‘local’ currencies of sensory hedonics might, in principle, be combined [21] to derive a value Gestalt, with unique weights assigned to each modality depending on the context.

When subjects have to evaluate the overall attractiveness of an object that differs in terms of its visual esthetic and semantic properties, their decision is guided by combining attribute-specific values [49]. The attribute-specific values, in turn, may be computed in perceptual areas specialized for the processing of a given stimulus feature and then passed on to the OFC and ventromedial prefrontal cortex [52], where ultimately overall value is assigned, supporting a common currency of pleasantness.

Future research directions

Future research will need to explicitly test the ideas offered here. A useful strategy would be to use methods like RSA to probe the geometry of information supported within a brain area to address the existence of common (supramodal) valence codes and to determine whether valence codes are interleaved within sensory specific object representations. Neuroimaging methods with adequate resolution (high density M/EEG) can be leveraged to obtain spatiotemporal portraits of basic affective categorizations in different modalities. A similar strategy has been used to demonstrate that high-level (non-affective) semantic categorizations are spatiotemporally co-localized with low-level visual representations [53]. Conditioning models can also be used to study experience-dependent plasticity mechanisms that we have proposed [18] store reward/punishment histories directly in sensory cortices ([54•], see also [9, 24, 55, 56]). A new understanding of the multiplicity of neural representations of affect should make novel predictions for perception and action. For instance, might judgments of perceptual similarity be shaped by affective similarity in ways that align perception, decision making and action?

Conclusion

Perception evolved not so much to objectively represent the exterior world but as an elaborate set of error-correcting mechanisms for controlling behaviors aimed at satisfying essential biological needs [3–5]. Affective influences on perception are usually studied from the perspective of top-down biases that originate from heteromodal brain regions and reach down to enhance sensory detection and/or discrimination. We propose that, in addition to these well-established effects, some attributes of hedonic valence are contained directly within sensory cortices, sharing a status similar to other perceptual or categorical dimensions within a given modality. This raises the intriguing possibility that the pleasantness of a percept is no more an extraneous gloss painted over sensations than experienced shades of color are painted over visual sensoria. Just as the sky is construed as blue by our visual system, phenomenal objects may be perceived as good or bad, linking perceptions to movements toward or away from them in corresponding measure.

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Highlights

- We consider whether sensory areas directly maintain population codes of valence.
- Brain imaging evidence suggests some valence representations are not shared across senses.
- Modality-specific valence may support high-dimensional evaluation of stimuli.

Figure 1.

Inferring the existence of a shared, modality-general valence code based on regional overlap from traditional univariate approaches can miss the microstructure of underlying brain response. **(a)** Conventional analyses of the magnitude of univariate activity in the orbitofrontal (OFC) and ventromedial prefrontal cortices show substantial overlap (green) of regional activity coupled to extremity of both positive (yellow) and negative (blue) valence. **(b)** Despite regional overlap, a trial-by-trial analysis of multivariate patterns demonstrates that valence distance is supported in the posterior ventral temporal cortices (VTC) and to an

even greater degree in OFC as depicted by multidimensional scaling of patterns evoked by each picture (color coded by experienced valence). The geometry of multivoxel patterns supports the valence spectrum, with pictures associated with positive and negative experiences furthest apart in this space. **(c)** To establish supramodal coding, valence of different modalities must be coded similarly, where the local distribution of those neurons is the same. Similarity-dissimilarity of activation patterns within modalities (across pictures) is extended between modalities (e.g. visual $\times$ gustatory) in a region-specific manner. While OFC valence distance did meet this criterion, corresponding across vision and taste, this was not the case for the VTC, which coded visual valence but not taste. **(d)** While population codes in the medial OFC supports valence distance in vision, gustation, and across vision and gustation, valence codes were selective for pictures in the VTC and liquids in the anterior insular (aINS) cortex. This provides evidence to sensory specific valence codes in visual and gustatory cortices. Bar height indicates correspondence between multivoxel patterns and subjective experienced valence.

Figure adapted from [17•].

Figure 2.

Information about the hedonic properties of stimuli in the external world may be embedded directly within the posterior sensory cortical areas. In panel (a) (*left*), a population code of hedonic valence is represented in a schematic multidimensional scaling plot, with an axis that reflects the relative degree of pleasantness. An idealized representational similarity matrix of hedonic valence (panel a, *right*) indicates greater population-level activity pattern correlations with increasing valence similarity. In panel (b), modally bound representations of hedonic valence are translated into a common, supramodal code of valence that is lower in dimensionality than each of the respective modality-specific representations. In principle, differential weights can be assigned to the hedonic code originating from a specific modality in order to bias responses to complex, multifaceted stimuli.