

## Linguistic priors shape categorical perception

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### ABSTRACT

This article reviews recent literature on the role of top-down feedback processes in semantic representations in the brain. Empirical studies on perception and theoretical models of semantic cognition show that sensory input is filtered and interpreted based on predictions from higher order cognitive areas. Here, we review the present evidence to the proposal that linguistic constructs, in particular, words, could serve as effective priors, facilitating perception and integration of sensory information. We address a number of theoretical questions arising from this assumption. The focus here is if linguistic categories have a direct top-down effect on early stages of perception; or rather interact with later processing stages such as semantic analysis. We discuss experimental approaches that could discriminate between these possibilities. Taken together, this article provides a review on the interaction between language and perception from the predictive perspective, and suggests avenues to investigate the underlying mechanisms from this perspective.

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### Introduction

The human conceptual system supports meaningful interaction with the environment, by affording object recognition and guiding our perception and action. In the last two decades, neuroimaging research on the neural basis of concepts has shown that recognition of objects and comprehending words involves reactivation of sensory-motor representations that emerge through experience. Despite the large amount of empirical data, however, the relationship between the sensory-motor and conceptual representations is still debated. In particular, it is not clear to what extent this relationship is unidirectional, meaning that sensory and motor experiences form our conceptual knowledge, or bi-directional, which would mean that conceptual and linguistic categories, in turn, modulate our perception. This question has become particularly relevant since in the last decennium theoretical and experimental research (Barlow, 1990; Clark, 2013; Summerfield & de Lange, 2014) has suggested that perception is not a passive process driven purely by bottom-up information but rather is actively driven in a top-down fashion by predictions about the environment. In this review article, we will consider the existing literature on top-down effects in multimodal perception and semantic cognition, and we will specifically focus on the role of language as one of the possible top-down factors, constraining perception.

### Grounded cognition and multimodal integration

It has long been suggested that conceptual knowledge is mapped within the brain sensory-motor system (Allport, 1985; Barsalou, Kyle Simmons, Barbey, & Wilson, 2003; Chao, Haxby, & Martin, 1999; Gallese & Lakoff, 2005; Kiefer & Pulvermüller, 2012). A large number of neuroimaging studies have shown activation of sensory or motor cortices when participants are engaged in language and semantic tasks related to sensory or motor concepts. For instance, subregions of the ventral temporal cortex that process colour information are activated when people generate words denoting colours (Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995), or read words with strong colour associations, such as the word “banana” or “light bulb” (Simmons et al., 2007). Likewise, generation of action words activates brain areas involved in perception of motion (Martin et al., 1995), and reading action verbs results in activations in motor and pre-motor cortices, at locations that are very close to the corresponding motor representations (Hauk, Shtyrov, & Pulvermüller, 2008) and in visual motion areas (Wallentin et al., 2011; Wallentin, Weed, Østergaard, Mouridsen, & Roepstorff, 2008). These findings indicate that concepts are functionally and anatomically linked to sensory and motor areas of the brain.

At the same time neuroimaging studies on semantic processing report with remarkable consistency large portions of the brain that are not implicated in sensory and motor processing but yet are activated during semantic tasks (reviewed by Binder & Desai, 2011; Binder, Desai, Graves, & Conant, 2009; Martin, 2007). It has been proposed that certain parts of the cortex serve as convergence zones (“hubs”), integrating information from “spokes”, i.e. visual, auditory, somatosensory, gustatory/olfactory, motion, emotional, and action attributes of concepts, into increasingly abstract representations (Binder & Desai, 2011; Damasio, 1989; Patterson, Nestor, & Rogers, 2007; Rogers et al., 2004).

The systematic binding of sensory information, which is required according to the “hub and spokes” model of semantic organisation, has long been seen as the foundation for forming concepts (Barsalou, 1999; Damasio, 1989; Man, Kaplan, Damasio, & Damasio, 2013; Martin, 2007). Neuroimaging studies on multimodal object recognition highlight three multisensory convergence areas: the posterior superior temporal sulcus (STS) and superior temporal gyrus (STG) for audiovisual integration, the ventral lateral occipital complex (LOC) and intra-parietal sulcus (IPS) for visual-tactile integration (Man et al., 2013). Fernandino et al. (2015) have recently confirmed the involvement of these brain areas in semantic processing. The authors explored functional magnetic resonance imaging (fMRI) activations associated with five sensory-motor attributes – colour, shape, visual motion, sound, and manipulation for concrete and abstract words. The patterns of fMRI responses for 900 studied words indicate that these attributes are encoded at secondary sensory and multimodal convergence areas. For instance, the lateral occipital complex is involved in processing of words that are associated with both haptic and visual attributes. Fernandino and colleagues build on the existing “hub and spokes” model and suggest a hierarchical structure of conceptual knowledge, in which unimodal sensory areas at the lowest level pass information to secondary sensory and then to bimodal and trimodal convergence zones,<sup>1</sup> followed by higher-level multimodal association areas. The cortical hubs of the highest level, activated by all attributes, are located in the angular gyrus, precuneus/posterior cingulate/retrosplenial cortex, parahippocampal gyrus, and medial prefrontal cortex. The model suggests that neuronal circuits in these regions form an increasingly abstract representation of an entity, which agrees with previous studies on the multimodal object recognition and semantic processing (Binder & Desai, 2011; Binder et al., 2009; Man et al., 2013).

### Top-down effects in multimodal perception and conceptual processing

At present, most theories discussing the role of the sensory-motor system in conceptual knowledge consider primarily the bottom-up processing of information from different sensory sources. At the same time, there is a vast literature on the modulatory effects from higher order cortices towards earlier sensory cortices. One of such top-down factors, which has been prominent in the research on multisensory integration, is the expectation of co-occurrence of sensory events. Multiple studies have shown that multimodal recognition is modulated by prior expectations on whether sensory signals should be combined or segregated (Molholm, Martinez, Shpaner, & Foxe, 2007; Murray et al., 2004; Naci, Taylor, Cusack, & Tyler, 2012). As an example of such a study, Lee and Noppeney, 2014 explored top-down effects in multisensory integration. Participants were presented with audiovisual movies that were either synchronous or asynchronous (visual leading or auditory leading). They found that visual leading relative to synchronous movies increased activations in the auditory system, while auditory leading relative to synchronous movies increased activations in bilateral occipital-temporal cortices. The authors explain this double dissociation by a bidirectional (auditory-to-visual and visual-to-auditory) top-down mechanism operating via convergence areas such as STG/STS. These findings suggest that multisensory integration is afforded by top-down activation of multiple sensory systems under an expectation about objects in the world, which affects early unimodal processing of object features.

Given the link between the multisensory integration and conceptual processes, reviewed above, we believe that present theories of neurobiology of conceptual processing could be complemented by a clear discussion of the role of top-down information in the organisation of perceptual input. Several theoretical models attempt to explain how bottom-up perceptual evidence and top-down expectations together define perception. One of the most influential models in neuroimaging research these days is the predictive coding model (Clark, 2013; Friston, 2003; Hohwy, 2013). According to this model, predictions, or priors, on the perceptual input are represented at all levels of the perceptual hierarchy, with greater complexity at higher stages (Summerfield & de Lange, 2014). Inference at each level of the hierarchy occurs when top-down prediction signals are compared with bottom-up sensory evidence, which leads to a prediction error signal that flows forward. This updating occurs repeatedly and

drives the update of the priors (Rao & Ballard, 1999; Summerfield & de Lange, 2014). The predictive coding framework has become increasingly popular, since it provides a mechanistic explanation for a number of well-known phenomena such as repetition suppression (Kok, Jehee, & de Lange, 2012; Segaert, Weber, de Lange, Petersson, & Hagoort, 2013), visual responses to illusory contours, motion illusions, and binocular rivalry (Hohwy, 2013; Hohwy, Roepstorff, & Friston, 2008; Summerfield & de Lange, 2014).

In his general commentary (Lupyan, 2012a) on Andy Clark's article on predictive coding (Clark, 2013), Gary Lupyan argues that in the human conceptual system verbal labels (names) could serve as predictive category cues, augmenting the processing of incoming sensory information and resulting in a more efficient discrimination between perceptual categories. Living in a language environment and the permanent use of linguistic labels require humans to engage in rapid implicit categorisation all the time. In Lupyan's view, naming shifts perception, such that features that are diagnostic for the labelled category are highlighted, while within-category differences are minimised (Lupyan, 2012b; Perry & Lupyan, 2014). Thus, categorical distinctions learned via words could provide immediate online effects on sensory perception (Brouwer & Heeger, 2013; Lupyan, 2012a; Lupyan & Spivey, 2008; Lupyan & Thompson-Schill, 2012).

Yet, whether the interaction between language-based categories and sensory perception could be explained by a predictive mechanism is still an open question. Several computational models of perception, such as the biased competition model of visual attention (Desimone, 1998; Desimone & Duncan, 1995) and mutual constraint satisfaction (McClelland & Rumelhart, 1981; McClelland, Mirman, Bolger, & Khaitan, 2014) are highly similar in some aspects to predictive coding, and give similar predictions on neural effects. It is thus often problematic to discriminate the predictive coding account from other mechanistic implementations of feedback–feedforward interactions in the brain, and discussing these differences is beyond the scope of this review. Here we consider two implications that follow from the predictive coding model and similar models. First, the predictive account would suggest that language modifies neural responses at each level of perceptual processing, including the responses in early sensory areas (spatial assumption). Second, predictive coding implies that top-down expectations evoke changes in neural activity before as well as during the presentation of a stimulus (temporal assumption). Let us consider the present neuroimaging evidence for these assumptions.

## Evidence for an interaction between language and perception in sensory areas

Several studies explored the interaction between language and perception with fMRI. Puri, Wojciulik, and Ranganath (2009) used words (either “face” or “house”) to prime the perception of pictures of faces and houses. They compared activations in the category-selective regions of extrastriate cortex (fusiform face area [FFA] and parahippocampal place area [PPA], respectively) for expected (congruent with the prime) versus unexpected (incongruent with the prime) stimuli. They found that the difference in activity between preferred and non-preferred stimuli for both category-selective regions was higher for expected stimuli. Thus, the language primes facilitated visual perception, by increasing the category selectivity for expected stimuli.

Another recent fMRI study looked systematically at the effect of language on perception of colours at different levels of the visual hierarchy, from V1 to the object-recognition regions in the extrastriate cortex (Brouwer & Heeger, 2013). Participants were presented with 12 different colours, sampled uniformly from the colour space. In the naming condition participants had to name the colours, while in the control condition they performed an attention task with the same stimuli, which did not require colour discrimination. The neural responses to colours in the area V4 and lateral occipital cortical area VO1 were clustered according to the subjective colour categories, i.e. greater similarity was shown for activity patterns evoked by colours within same category, compared to between-category colours. Notably, this clustering effect only emerged in the naming condition (Brouwer & Heeger, 2013). However, with the tasks used by the authors, it is difficult to discriminate the effects of language from those of attention, because the colour-naming task was contrasted with a condition where no attention to colour was required.

Taken together, these two studies provide evidence for top-down facilitation of visual perception by language. A possible neural mechanism that could explain this top-down effect has been suggested by the sharpening model of expectation (Kok et al., 2012) or priming (Grill-Spector, Henson, & Martin, 2006). Under this model, higher order cortical regions sharpen sensory representations in early regions by suppressing neural responses that are inconsistent with current expectations. The studies by Puri et al. and Brouwer and Heeger demonstrate the sharpening effect of language in regions of the visual stream that are specific for processing of complex visual features: region V4 for colours (Brouwer & Heeger, 2013) and FFA and PPA for object categories (Puri et al., 2009).

At the same time, other studies found no direct evidence for the interaction between language and visual perception in the visual processing stream. In a study by Francken, Kok, Hagoort, and de Lange (2015) participants performed a motion detection task, where the motion stimuli were primed with motion words. The authors found that when motion words were congruent with the direction of visual motion stimuli, participants were more accurate in detecting visual motion. The priming effect (a greater activation for congruent versus incongruent primes) was found in the left middle temporal cortex; however, no significant effect of word congruency was found in motion-selective areas of the visual cortex. Similarly, Tan et al. (2008) studied neural activation associated with a perceptual decision task for easy-to-name versus difficult-to-name colours. Significantly higher activation during discrimination of easy-to-name, compared to hard-to-name colours was found in the left posterior STG and in the left inferior parietal lobe. The authors indicate that these regions are involved in colour naming, according to a localiser task used in their experiment. Therefore, perceptual discrimination of colours activates regions that also contribute to language-based colour categorisation even when no colour naming is required. At the same time, similar to the results of Francken et al. (2015), no effect of linguistic labels was found in the areas of visual processing.

Together, the present fMRI studies remain inconclusive on whether language modulates perception in sensory areas of the brain. While several studies have demonstrated such language–perception interactions in the visual cortex, others find no evidence for this hypothesis. A possible explanation for the latter results would be that language does not constrain early perception in a predictive way, but rather interacts with later processing stages such as categorical decision-making.

Another type of insight on the level of the interaction between language and perception comes from studies using electrophysiological methods. It has been reported that native vocabulary modulates event-related responses to visual stimuli at early time intervals (Hirschfeld, Zwitserlood, & Dobel, 2011; Mo, Xu, Kay, & Tan, 2011; Thierry, Athanasopoulos, Wiggett, Dering, & Kuipers, 2009). For example, Mo et al. (2011) studied the visual mismatch negativity (vMMN) effect, which is a component of the event-related potential in response to an unexpected stimulus. They presented participants with pairs of colour stimuli either from the same category (green + green, blue + blue), or from different categories (green + blue). A significantly larger vMMN at 130–190 ms was evoked by a mismatching stimulus from a different category compared to a mismatching stimulus from

the same category, despite the identical perceptual distance between the colours in both conditions. This effect was observed only when stimuli were present in the right visual field, indicating the involvement of the left language-dominant hemisphere. The authors interpret this finding as an early pre-attentive effect of language on categorical perception of colour (Mo et al., 2011). Thierry et al. (2009) compared the event-related responses to colour stimuli in native Greek and English speakers, who have different colour vocabularies. Speakers of Greek use special colour terms for light and dark shades of blue. Such a distinction between shades of blue does not exist in English. Similarly to Mo et al. (2011), Thierry and colleagues studied the vMMN response to mismatching colour shades for green and blue stimuli. The vMMN effect was significantly larger for blue versus green mismatching stimuli for Greek participants. The effect was not found in English participants. The study concludes that the existence of specific terms in the colour vocabulary accounts for better early discrimination between different colour shades.

### **Evidence for pre-stimulus language-driven modulations of activity in sensory areas**

The second assumption of the predictive coding model concerns the timing of the prediction effect. Under predictive coding, expectations should modulate the activation level in the sensory cortex before the stimulus-evoked activity. However, very little is known about pre-stimulus effects of language on perception. To our knowledge, only one fMRI study, already mentioned above, has shown such an effect for language-driven categorical expectations (Puri et al., 2009). In the experiment, expectations were set by words (“face”, “house”), which were predictive to the category of the subsequent target image. The authors found that activity in the FFA and PPA was increased during expectation of an image from the preferred versus non-preferred category.

Studies of oscillatory electrophysiological activity give an opportunity to study the neural correlates of predictive processing before the stimulus is presented. Based on electrophysiological studies in the visual system of humans and monkeys, it has been suggested that top-down predictions are mediated by slower frequencies (theta: 4–7 Hz, and beta: 15–30 Hz), while bottom-up prediction errors are mediated by higher frequencies (gamma: 25–40 Hz). Several studies on auditory speech perception have confirmed this notion for the language domain (Arnal, Wyart, & Giraud, 2011; Lewis & Bastiaansen, 2015; Sohoglu, Peelle, Carlyon, & Davis, 2012). In a magnetoencephalography experiment,

Dikker and Pykkänen (2013) used pictures of either specific objects (predictive context), or groups of objects (non-predictive context) to constrain the probability of occurrence of certain words in a sentence. In line with the assumption on the existence of pre-stimulus predictive activity, the authors showed an increased signal in the theta range before presentation of a word in a predictive context. This theta rhythm increase was registered in a number of brain areas, including the left mid-temporal cortex, ventral-medial prefrontal cortex, and visual cortex. It is unknown, however, whether the opposite direction of priming (from prime words to target pictures) would elicit the same effect.

### The origin of language-generated predictions

Although there exists no direct evidence on where the top-down language effects originate in the brain, the present data allow for discussing several plausible candidates.

The *left Middle Temporal Cortex* has long been associated with lexical access, i.e. linking phonological and semantic information (Binder & Desai, 2011; Hickok & Poeppel, 2007; Snijders et al., 2009). The congruency effects evoked by language-generated expectations in this region, shown by Francken et al. (2015) and Dikker and Pykkänen (2013), support the notion on the involvement of this region in language-mediated categorical expectations. Several studies reported identical activation patterns in posterior MTG/ITG for linguistic and non-linguistic stimuli (Fairhall & Caramazza, 2013; Simanova, Hagoort, Oostenveld, & van Gerven, 2014), suggesting that both visual/auditory objects and their names (both spoken and written) can access the representation of conceptual content in this region.

Another question that has hardly been addressed by previous research is the role of the *Prefrontal Cortex* in language–perception interactions. Adam and Noppeney (2014) propose that priors might affect multisensory integration through modulatory activity in the left prefrontal cortex, as has previously been implicated in cognitive control. Interestingly, Binder and Desai (2011) include prefrontal regions in their model of neurobiology of semantic memory. They suggest that portions of the prefrontal cortex are functionally connected to the pMTG/ITG and the parietal hub and are critically involved in semantic processing. According to their model, dorsomedial prefrontal cortices and anterior and ventral aspects of the inferior frontal gyrus provide top-down control on semantic storage and coordinate goal-directed selection and retrieval of conceptual knowledge. From the predictive perspective, prefrontal areas could be seen representing the top level of the hierarchy,

leading to downstream activations of conceptual areas in temporal cortex and ultimately in early sensory areas (deWit, Machilsen, & Putzeys, 2010).

### Summary

In this article, we discuss the interaction between top-down and bottom-up information processing streams in the organisation of conceptual knowledge in the brain. Does our conceptual knowledge shape our perception of the world? Here, we review the assumption that language-mediated categories could be considered as one of the top-down factors that constrain sensory perception. We show that linguistic categories modulate perception at the level of secondary sensory areas, and at the level of convergence of multimodal sensory information, and that the sharpening model (Grill-Spector et al., 2006; Kok et al., 2012) can explain some of the reported data on language–perception interactions. Other studies, however, show no evidence for a direct influence of language on perceptual processing, but rather show effects of language-mediated expectations in lexical access areas of the brain. Furthermore, the present studies remain inconclusive on whether language–perception interaction effects extend to early sensory cortices, and whether language affects pre-stimulus activity in sensory areas. Thus, the timing aspects and the neurophysiological mechanisms of language–perception interactions still require clarification.

### Disclosure statement

No potential conflict of interest was reported by the authors.

### Note

1. Although the existence of trimodal convergence zones is questioned by other researchers, see Man et al. (2013).

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