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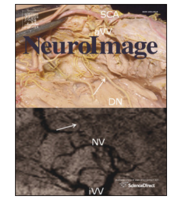

The context-contingent nature of cross-modal activations of the visual cortex

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ABSTRACT

Real-world environments are nearly always multisensory in nature. Processing in such situations confers perceptual advantages, but its automaticity remains poorly understood. Automaticity has been invoked to explain the activation of visual cortices by laterally-presented sounds. This has been observed even when the sounds were task-irrelevant and spatially uninformative about subsequent targets. An auditory-evoked contralateral occipital positivity (ACOP) at ~250 ms post-sound onset has been postulated as the event-related potential (ERP) correlate of this cross-modal effect. However, the spatial dimension of the stimuli was nevertheless relevant in all prior studies where the ACOP was observed. By manipulating the implicit predictability of the location of lateralised sounds in a passive auditory paradigm, we tested the automaticity of cross-modal activations of visual cortices. 128-channel ERP data from healthy participants were analysed within an electrical neuroimaging framework. The timing, topography, and localisation resembled previous characterisations of the ACOP. However, the cross-modal activations of visual cortices by sounds were critically dependent on whether the sound location was (un)predictable. Our results are the first direct evidence that this particular cross-modal process is not (fully) automatic; instead, it is context-contingent. More generally, the present findings provide novel insights into the importance of context-related factors in controlling information processing across the senses, and call for a revision of current models of automaticity in cognitive sciences.

Introduction

The multisensory nature of real-world environments provides obvious benefits for object recognition and goal-directed behaviour. In social situations, with many people speaking, seeing lip movements of the next speaker helps us know where to attend and to understand what will be said next (e.g., van Wassenhove et al., 2005; Zion-Golumbic et al., 2013). Notwithstanding, in laboratory settings even simple sounds are shown to modulate the brain processing and/or facilitate perception of visual objects. At least two prominent types of processes contribute to these effects: multisensory integration of information (reviewed in Ghazanfar and Schroeder, 2006; Stein, 2012; Murray and Wallace, 2012) and orienting of spatial attention to the sound location (McDonald et al., 2000, 2003, 2012; Störmer et al., 2009; reviewed in Koelewijn et al., 2010; Hillyard et al., 2015). Importantly, each of these processes is subject to a differing degree to constraints imposed by the current behavioural goals of the observer, which will determine the efficacy of a particular cross-modal influence. While at least some multisensory processes, such as those based on the detection of multisensory simultaneity, occur independently of the task-relevance of the other-modality signals (Matusz and Eimer, 2011; De Meo et al., 2015; Murray et al., in press; Ten Oever et al., in revisions), orienting of involuntary spatial attention might be less impervious to it.

It has been well established within the area of visual attention that even perceptually salient stimuli, if task-irrelevant, fail to attract involuntary shifts of spatial attention (task-set contingent attentional capture; Folk et al., 1992; reviewed in Nobre and Kastner, 2014). This was confirmed by experiments employing brain response measures. Functional magnetic resonance imaging (fMRI) studies have consistently demonstrated that the ventral fronto-parietal brain network that serves as the 'circuit breaker' for the ongoing goal-driven behaviour (i.e., it reorients attention) responds predominantly, if not exclusively, to 'irrelevant' stimuli as long as these stimuli share features with the target (reviewed in Corbetta and Shulman, 2002). Notably, fMRI evidence has suggested that there are no differences across sensory modalities in engaging the ventral attentional network (in, typically visual, spatial attention tasks; e.g., Downar et al., 2000). However, with their sub-

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millisecond resolution, event-related potentials (ERPs) might be a method particularly well-suited to study fast-paced, attentional process (e.g., Ding et al., 2014). In line with the behavioural and hemodynamic evidence, ERP studies in visual attention have demonstrated that distracters in spatial attention tasks elicit brain responses indicative of top-down suppression (distracter positivity, Pd), rather than attentional selection (the N2pc component), of those distracters in space (Hickey et al., 2009; Sawaki and Luck, 2010; Wykowska and Schubö, 2010, 2011; McDonald et al., 2012; Gaspar and McDonald, 2014). These findings have jointly suggested that in real-world environments stimuli not matching the current goals of the observer have little ability to attract the observer's attention (with the exception, maybe, of stimuli whose task-relevance is ‘hardwired’ in the brain; e.g., Koster et al., 2004; Humphreys and Sui, 2015; Matusz et al., 2015a; Munneke et al., 2015).

Research that employed stimuli from different sensory modalities within visual spatial-attention tasks has been intimating a more nuanced view on this issue. In one exemplary behavioural study, a short sound to the left or right was shown to facilitate perception, as indexed by d′, of a faint LED array flash appearing subsequently at the sound location (McDonald et al., 2000). Importantly, a recent pair of studies revealed the likely brain substrates of this cross-modal perceptual benefit. Across a series of experiments, involving both auditory and visual targets, lateralised sounds that preceded these targets were found to elicit positive-going potentials over the contralateral occipital scalp starting at approximately 250 ms post-stimulus (ACOP; McDonald et al., 2013a, 2013b; Feng et al., 2014). The positive links between the ACOP amplitude and both subjective and objective measures of perceptual processing, on the one hand, and the fact that the sounds were not predictive (i.e., informative) of target locations, on the other hand, are consistent with shifts of exogenous, involuntary spatial attention underlying the observed cross-modal perceptual benefits (Hillyard et al., 2015).

The task-irrelevance of the ACOP-inducing sounds and the robustness of their effects in perception have opened the possibility that the ACOP, and the exogenous attention orienting it might reflect, is ‘automatic’ in nature (McDonald et al., 2013a, 2013b). The Miriam-Webster online dictionary defines ‘automatic’ as a quality: “(…) that allow[s] something to work or happen without being directly controlled by a person”. Similarly, a recent review of several models of automaticity as a concept in cognitive research (Moors and de Houwer, 2006) highlights that an automatic process is typically characterised by “features, such as unintentional, uncontrolled/uncontrollable, goal-independent, autonomous, purely stimulus driven, unconscious, efficient, and fast” (p. 297). Both sources, thus, emphasise predominantly the involuntary nature of an ‘automatic’ process. The question of automaticity of involuntary shifts of spatial attention is, as we described, hardly new. However, it regains its importance and novelty when considered more broadly, in real-world environments. Here, the multitude of channels providing sensory inputs is mirrored by the multitude of top-down mechanisms that control sensory processing (Doehrmann and Naumer, 2008; Summerfield and Egner, 2009; Nobre and Kastner, 2014). The study of brain and/or cognitive processes at the intersection of these bottom-up and top-down influences, while insurmountable at a first glance, is both feasible and timely; the necessary background has been created by the traditional research involving rigorous experimental setups with unisensory (visual or auditory) stimulation. At the same time, such investigations bring us closer to understanding the information processing as it occurs in situations more closely resembling naturalistic environments.

One notable feature linking all previous empirical reports of the ACOP is that this component has been observed exclusively in response to task-irrelevant sounds that were spatially unpredictable. This opens the possibility that while the ACOP might indeed occur involuntarily, it depends on the stimulus context. The context can be understood as the “immediate situation in which the brain operates” (van Atteveldt et al., 2014) and, more specifically, the observer's expectations. If the circumstances in which the sounds are presented, such as how (un)predictable the sound location is, determine the presence of the ACOP, this would speak against the automaticity of this particular brain/cognitive process. More generally, this would call for a revision of the existing conceptualisations of automaticity of cognitive processes.

While task-relevance is one frequently studied form of top-down control over sensory processing, within (reviewed in Nobre and Kastner, 2014) and across the senses (e.g., Matusz and Eimer, 2011, 2013; reviewed in Talsma et al., 2010; De Meo et al., 2015; Ten Oever et al., in revisions), an increasing number of studies points to similar importance of context-based influences. As demonstrated by traditional, unisensory studies, context influences range from predictions (Summerfield and Egner, 2009), through external and internal states (e.g., remembering something better in a place where one had learnt it), to fine-grained differences in stimulus features (e.g., the object's colour; Bar, 2004; Baddeley et al., 2009). These can affect the activity across scales from a single neuron (reviewed in Gilbert and Li, 2013) to whole-brain cognitive functions, including auditory stimulus parsing, visual search or conditioning (e.g., Saffran et al., 1996; Baker et al., 2004; Courville et al., 2006; Goujon and Fagot, 2013). More recently, the context has been revealed as an important source of top-down control over processing of multisensory information. While some studies demonstrated the role of long-term experience and learning (e.g., Froyen et al., 2009; Stevenson and Wallace, 2013; Barenholtz et al., 2014; Ten Oever et al., 2014; Matusz et al., 2015b), many focused on effects operating at shorter timescales, such as expectations and/or experiences built over the course of a single experimental session (e.g., Murray et al., 2004, 2005; von Kriegstein and Giraud, 2006; Meylan and Murray, 2007; Rosenblum et al., 2007; Beierholm et al., 2009; Powers et al., 2009; Barakat et al., 2013; Chandrasekaran et al., 2009; Thelen et al., 2012, 2014; Matusz et al., 2015c; Altieri et al., 2015), or even across a pair of successive experimental trials (Wylie et al., 2009; Murray et al., 2009; King et al., 2012; Sarmiento et al., in press). Considered together, the overwhelming evidence for the importance of context-based factors for stimulus processing across the senses and the concomitant limited existing data on the ACOP makes it plausible that irrelevant sounds activate the visual cortex in some contexts but not in others. Verifying the sensitivity of the ACOP to context-based influences defined as expectations was, thus, at the centre of the present study.

More specifically, we investigated whether the ability of irrelevant lateralised sounds to trigger the ACOP depends on the implicit predictability of the location of these sounds. If the presence of the ACOP indeed depends on the unpredictability of the sound location, this would provide strong evidence against the automaticity of these cross-modal activations, as an automatic process would be expected to occur independently of the circumstances. Findings indicative of such sensitivity would likewise have broader implications, in that they would call for consideration and inclusion of top-down control mechanisms based on context in future studies of automaticity of brain and cognitive processes and, more broadly, theoretical models of automaticity within the cognitive sciences. To test our hypothesis, we employed a passive ‘oddball’ paradigm and measured ERPs elicited by lateralised sounds that were presented while participants watched a muted, subtitled movie. Critically, in some blocks (‘spatially irregular contexts’) sounds were presented equi-probably to the left versus the right hemispace, while in others (‘spatially regular contexts’) sounds were located predominantly (80% trials) within one of the two hemispaces (Fig. 1). The passive setup was employed to further ensure the task-irrelevance of the activation-inducing sounds; in virtually all of the previous reports of the ACOP, the irrelevant sounds that elicited it shared with the targets the lateralised nature of their presentation. This could have rendered the former being perceived as potential targets and thus (rudimentarily) task-relevant. To foreshadow our findings, we have indeed found clear evidence that in our passive paradigm the

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