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Perceptual load influences auditory space perception in the ventriloquist aftereffect

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ABSTRACT

A period of exposure to trains of simultaneous but spatially offset auditory and visual stimuli can induce a temporary shift in the perception of sound location. This phenomenon, known as the 'ventriloquist aftereffect', reflects a realignment of auditory and visual spatial representations such that they approach perceptual alignment despite their physical spatial discordance. Such dynamic changes to sensory representations are likely to underlie the brain's ability to accommodate inter-sensory discordance produced by sensory errors (particularly in sound localization) and variability in sensory transduction. It is currently unknown, however, whether these plastic changes induced by adaptation to spatially disparate inputs occurs automatically or whether they are dependent on selectively attending to the visual or auditory stimuli. Here, we demonstrate that robust auditory spatial aftereffects can be induced even in the presence of a competing visual stimulus. Importantly, we found that when attention is directed to the competing stimuli, the pattern of aftereffects is altered. These results indicate that attention can modulate the ventriloquist aftereffect.

1. Introduction

Exposure to spatially or temporally disparate stimuli from different sensory modalities can induce adaptation, resulting in a 'recalibration' between the modalities such that they tend to align in space or time. This phenomenon reveals the dynamic nature of sensory encoding, which is probably necessary to compensate for inter-sensory discrepancies caused by a wide range of factors such as variability in sensory transduction, biophysical properties leading to differences in neural transmission times, growth and development, and disease-related sensory impairment (King, 2005; Spence & Squire, 2003). Such cross-modal adaptation is exemplified by the ventriloquist aftereffect (Canon, 1970; Frissen, Vroomen, de Gelder, & Bertelson, 2003, 2005; Lewald, 2002; Radeau & Bertelson, 1974; Recanzone, 1998). This adaptation effect arises after exposure to synchronous auditory and visual stimuli presented with a consistent spatial disparity. Over a period of 10–20 min of such exposure (Canon, 1970; Frissen et al., 2003; Recanzone, 1998) auditory spatial representations presumably 'realign' to counteract the audiovisual spatial disparity, resulting in the observed systematic shift of auditory localization in the direction of the previously presented visual stimuli. Moreover, the shift persists for at least several minutes if no further audiovisual input is available to reset spatial alignment (Canon, 1970; Frissen et al., 2003; Radeau & Bertelson, 1974; Recanzone, 1998).

An important controversy regarding the mechanisms of multisensory integration (such as those underlying the ventriloquist aftereffect), is the degree to which they might operate automatically, without the need for focal attention (e.g., Macaluso & Driver, 2005; McDonald, Teder-Salejarvi, & Ward, 2001; Recanzone & Sutter, 2008; Talsma, Senkowski, Soto-Faraco, & Woldorff, 2010). Understanding how attention

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might influence the development of crossmodal spatial realignment is an important step towards elucidating the mechanisms of such short-term plastic processes, as well as multisensory integration in general. In an early study, Canon (1970) observed that when participants were instructed to preferentially attend to input from one sensory modality during adaptation, this could modulate the degree to which aftereffects were induced in the other modality. Typically, studies of the ventriloquist aftereffect only measure the aftereffects on auditory localization. However, adaptation also can lead to a small shift in the localization of visual stimuli towards the auditory stimulus (e.g., Canon, 1970; Lewald, 2002; Radeau & Bertelson, 1974). Canon (1970) found significant visual aftereffects when participants were instructed to attend the auditory input and ignore the visual stimuli during adaptation, whereas instructions to preferentially attend to visual input produced no visual aftereffects. Auditory aftereffects were, however, apparent under both attention conditions. Consequently, Canon noted that despite his instructions, participants had difficulty resisting distraction by the visual input in the attend-auditory condition. This difficulty highlights the need for a more effective manipulation by means of an attention-demanding task, for example. Nevertheless, the results suggest that attention may modulate the development of acoustically-induced visual aftereffects, but it is not clear whether selective attention influences the visually-induced *auditory* aftereffects.

Recently, Passamonti, Frissen, and Ladavas (2009) studied ventriloquist adaptation in patients with left spatial inattention following right temporo-parietal lesions. They reported that adaptation was equally effective in the unattended hemifield as in the attended hemifield of these patients. As is typically the case, when these patients were required to detect a single visual stimulus presented to either the left or right hemifield in preliminary testing, they showed poorer detection of left (18%) relative to right (100%) stimuli. After a period of audiovisual adaptation in which a visual stimulus in the neglected hemifield was paired with a spatially disparate (7.5°) auditory stimulus, the patients demonstrated significant auditory aftereffects that were of equivalent magnitude to aftereffects achieved following adaptation to a visual stimulus in the non-neglected right hemifield. Although this suggests that adaptation can be induced by an unattended visual stimulus, it is unclear from these results whether adaptation in the left hemifield actually occurred under conditions of reduced attention, because no direct unimodal visual attention test was performed under the *same* conditions as the adaptation trials. In particular, during adaptation, a single visual stimulus was presented in a predictable location on every trial, and patients had to actively monitor the visual stimulus for a subtle change in intensity. Left inattention is likely to have been diminished in the context of repeated targets in the same spatial location, and in the absence of any competing ipsilesional events (e.g., Driver, Mattingley, Rorden, & Davis, 1997; Mattingley et al., 2000).

Most studies of ventriloquist adaptation in neurologically normal participants have not directly investigated the role of attention in auditory aftereffects, although several have manipulated participants' attention to the adapting stimuli (Frissen et al., 2003; Lewald, 2002; Recanzone, 1998). These studies found no differential effects on the auditory aftereffect of attending to one modality over the other during adaptation. Typically, participants were required to direct their attention to either the visual or auditory stimulus of the audiovisual pair during adaptation by monitoring the stimuli for occasional changes in intensity. It must be noted, however, that by including these salient catch-trials only rarely within the paradigm (3–20% of trials), the attentional demand of these tasks was relatively low, and thus participants invariably performed at or near ceiling levels on them. Under such conditions of low attentional demand, it is likely that spare capacity was available to process the task irrelevant audiovisual pairs (see Lavie, 2005), thus potentially allowing successful adaptation.

The processing demands required to perform a task can modulate the degree to which other simultaneously presented stimuli are processed. According to Lavie's (2005) theory of perceptual load, a task requiring a difficult perceptual discrimination (high perceptual load) will reduce the attentional resources available to process peripheral, task-irrelevant stimuli. For example, increasing the perceptual load of a central visual task reduces exogenous orienting to irrelevant distractor stimuli (Cosman & Vecera, 2009; Lavie & Cox, 1997) and to peripheral cues on a secondary task (Santangelo, Finoia, Raffone, Olivetti Belardinelli, & Spence, 2008). Findings from fMRI studies indicate that allocating greater resources to a given high-load task leads to generalised suppression of neural activity related to peripheral, task-irrelevant stimuli and, presumably, to their processing (Montaser-Kouhsari & Rajimehr, 2004; Pinsk, Doniger, & Kastner, 2004; Rees, Frith, & Lavie, 1997; Schwartz et al., 2005). Increasing load also enhances activity related to attended targets in the load task (Pinsk et al., 2004). Thus, sensory processing that relies on selective attention is subject to competition for limited capacity resources.

In previous studies of the ventriloquist aftereffect, the visual stimulus used to 'capture' the sound was always presented in isolation, and was therefore free from potential competition from other concurrent visual events. Because selective attention acts to boost the processing of relevant inputs (e.g., Andersen, Hillyard, & Muller, 2008; Desimone & Duncan, 1995) and suppress those that are irrelevant (e.g., LaBerge & Brown, 1989; Lavie, 2005), attention is likely to have its greatest effect when there is competition from at least one concurrent visual input. Put another way, when there is more than one possible apparent source for a sound, directing attention to the relevant source may be critical for development of adaptation and the aftereffect. A similar point holds for previous studies of the ventriloquist *illusion*. The ventriloquist illusion is apparent when an observer's localization of a sound is biased towards a simultaneously presented but spatially disparate visual stimulus. Thus, unlike the ventriloquist aftereffect, the illusion is an ''immediate'' effect that occurs in the presence of visual stimulation. Most studies about the role of attention in the ventriloquist *illusion* have failed to find an effect of the direction of attention (Bertelson, Vroomen, de Gelder, & Driver, 2000; Vroomen, Bertelson, & de Gelder, 2001). In contrast,