Available online at www.sciencedirect.com

ScienceDirect

www.elsevier.com/locate/brainres

Brain Research

Research Report

Top-down controlled and bottom-up triggered orienting of auditory attention to pitch activate overlapping brain networks

Kimmo Alho[a,b,c,d,*], Juha Salmi[a,b], Sonja Koistinen[a], Oili Salonen[e], Teemu Rinne[a,b]

[a]Division of Cognitive Psychology and Neuropsychology, Institute of Behavioural Sciences, University of Helsinki, Finland
[b]Advanced Magnetic Imaging Centre, Aalto University, Finland
[c]Helsinki Collegium for Advanced Studies, University of Helsinki, Finland
[d]Swedish Collegium for Advanced Study, Sweden
[e]Helsinki Medical Imaging Center, Helsinki University Central Hospital, Finland

ARTICLE INFO

Article history:
Accepted 23 December 2014
Available online 31 December 2014

Keywords:
Top-down controlled
Bottom-up triggered
Attention
Auditory
Pitch
fMRI

ABSTRACT

A number of previous studies have suggested segregated networks of brain areas for top-down controlled and bottom-up triggered orienting of visual attention. However, the corresponding networks involved in auditory attention remain less studied. Our participants attended selectively to a tone stream with either a lower pitch or higher pitch in order to respond to infrequent changes in duration of attended tones. The participants were also required to shift their attention from one stream to the other when guided by a visual arrow cue. In addition to these top-down controlled cued attention shifts, infrequent task-irrelevant louder tones occurred in both streams to trigger attention in a bottom-up manner. Both cued shifts and louder tones were associated with enhanced activity in the superior temporal gyrus and sulcus, temporo-parietal junction, superior parietal lobule, inferior and middle frontal gyri, frontal eye field, supplementary motor area, and anterior cingulate gyrus. Thus, the present findings suggest that in the auditory modality, unlike in vision, top-down controlled and bottom-up triggered attention activate largely the same cortical networks. Comparison of the present results with our previous results from a similar experiment on spatial auditory attention suggests that fronto-parietal networks of attention to location or pitch overlap substantially. However, the auditory areas in the anterior superior temporal cortex might have a more important role in attention to the pitch than location of sounds.

This article is part of a Special Issue entitled SI: Prediction and Attention.

*Correspondence to: Institute of Behavioural Sciences, University of Helsinki, PO Box 9, FI 00014, Finland. Tel.: +358 40 5577578.
E-mail address: kimmo.alho@helsinki.fi (K. Alho).

http://dx.doi.org/10.1016/j.brainres.2014.12.050
0006-8993/

1. Introduction

We have an ability to direct our attention voluntarily to particular sounds or visual objects, for example, sounds and objects in certain location, sounds sharing a certain pitch or visual objects sharing a certain color (e.g., Näätänen, 1992; Pashler, 1997). However, even when we selectively attend to some auditory or visual inputs, our attention may be involuntarily caught by unpredictable or salient stimuli occurring outside the focus of our attention. Corbetta and Shulman (2002) have presented an influential model of partially segregated brain networks that are involved in voluntary, top-down controlled and in involuntary, bottom-up triggered orienting of visual attention. This model is based on brain imaging results and attention deficits in patients with local brain lesions and it suggests that the so-called dorsal attention system has a crucial role in top-down controlled attention shifts, for example, to the left or right visual field, while the gaze is kept directed forward. This dorsal system includes the intraparietal sulcus (IPS), superior parietal lobule (SPL), and frontal eye field (FEF). The so-called ventral attention system, in turn, is involved in bottom-up triggered attention to, for example, salient visual objects occurring in the lateral visual fields (cf. Posner et al., 1982). This ventral system includes areas in the temporo-parietal junction (TPJ, i.e., inferior parts of the inferior parietal lobule and posterior parts of the superior and middle temporal lobe) and posterior inferior/middle frontal gyrus (IFG/MFG).

Another attention model presented by Näätänen (1990, 1992) concerns voluntary and involuntary attention especially in the auditory modality. This model is largely based on event-related brain potential (ERP) studies in humans and it proposes that during voluntary orienting and maintenance of attention, prefrontal brain areas facilitate in a top-down manner processing of attended stimuli in sensory-specific cortical areas. This is also in accordance with our functional magnetic resonance imaging (fMRI) studies indicating that activity is enhanced in the lateral prefrontal areas and in the auditory cortex by sustained selective attention to tones at a particular location and by voluntary orienting of attention to such tones (Degerman et al., 2006; Salmi et al., 2007a; see also Alho et al., 1999). These fMRI studies have suggested that, in addition to prefrontal cortex, the posterior parietal cortex has a key role in auditory selective attention. According to Näätänen's model, involuntary attention may be caught by sounds causing enhanced afferent activity in the auditory cortex (e.g., tones in silence) or by deviant events breaking regularity in an auditory input stream and eliciting the mismatch negativity (MMN) response in ERPs (see also Näätänen and Winkler, 1999; Escera et al., 2000). Numerous fMRI studies have shown that in addition to enhanced activity in the auditory cortex, such deviant events are followed by enhanced prefrontal and parietal activity presumably associated with involuntary attention to these events (Molholm et al., 2005; Opitz et al., 2002; Rinne et al., 2005; Rinne et al., 2007; Schall et al. 2003; for auditory- and frontal-cortex contributions to the MMN, see Rinne et al., 2000; Yago et al., 2001).

Näätänen's (1990, 1992) model does not explicitly propose an overlap of brain networks for voluntary or top-down controlled and involuntary or bottom-up triggered auditory attention. However, our previous fMRI study (Salmi et al., 2009) applying tone streams similar to those used in many ERP studies showed a substantial overlap between these networks (see also Huang et al., 2012; Mayer et al., 2009). In our study, participants attended either to a stream of tones at the left or to a stream of tones at the right and performed a tone-duration discrimination task where they were to respond manually when duration of to-be-attended tones was changed. The participants were also instructed to shift their attention from one tone stream to the other when guided by

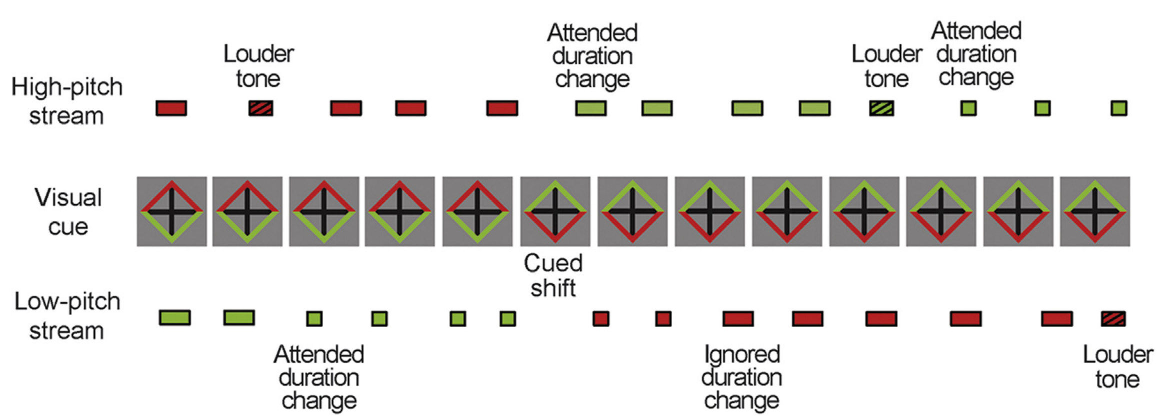

Fig. 1 – Experimental design. The participants were instructed to attend to a stream of tones with a higher pitch (perceived pitch at 1000 Hz) or to a stream of tones with a lower pitch (perceived pitch at 167 Hz) while ignoring the other stream. The stream to be attended (green rectangles) was indicated by a green arrowhead cue pointing up for attention to higher tones and down for attention to lower tones and the stream to be ignored (red rectangles) by the red arrowhead pointing up or down. Occasionally the cue changed and instructed the participants to shift their attention to the other stream (cued attention shifts). The participants' task was to press a button when they observed a change in the duration (from shorter 40-ms tones to longer 100-ms tones, or vice versa; tone durations indicated by the horizontal size of rectangles) of attended tones (attended duration changes). Duration changes occurred also in the to-be-ignored stream (ignored duration changes).
Task-irrelevant louder tones (striped rectangles) with a medium duration (70 ms) and with an increased intensity (+15 dB) occurred occasionally in both streams.