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Functional brain networks underlying idiosyncratic switching patterns in multi-stable auditory perception

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ABSTRACT

In perceptual multi-stability, perception stochastically switches between alternative interpretations of the stimulus allowing examination of perceptual experience independent of stimulus parameters. Previous studies found that listeners show temporally stable idiosyncratic switching patterns when listening to a multi-stable auditory stimulus, such as in the auditory streaming paradigm. This inter-individual variability can be described along two dimensions, *Exploration* and *Segregation*. In the current study, we explored the functional brain networks associated with these dimensions and their constituents using electroencephalography. Results showed that *Segregation* and its constituents are related to brain networks operating in the theta EEG band, whereas *Exploration* and its constituents are related to networks in the lower and upper alpha and beta bands. Thus, the dimensions on which individuals' perception differ from each other in the auditory streaming paradigm probably reflect separate perceptual processes in the human brain. Further, the results suggest that networks mainly located in left auditory areas underlie the perception of integration, whereas perceiving the alternative patterns is accompanied by stronger interhemispheric connections.

1. Introduction

Perceptual multi-stability (often referred to as bi-stability) refers to the phenomenon when perception stochastically switches between possible interpretations of an unchanging stimulus (for a review see Schwartz et al., 2012). It has been found that individuals vary in the frequency of switching both for visual (Aafjes et al., 1966) and auditory multi-stable stimuli (Kondo et al., 2012). Recently, idiosyncratic switching patterns have been found for verbal transformations (Kondo et al., 2017) and in the auditory streaming paradigm (Denham et al., 2014; Farkas et al., 2016a; Kondo et al., 2017). The latter have been linked to personality traits, executive functions (Farkas et al., 2016a), and neurotransmitter concentrations (Kondo et al., 2017). Using concurrent electroencephalogram (EEG) measures, the current study investigated for the first time the relationship between idiosyncratic switching patterns and functional brain networks activated while participants listened to an auditory streaming stimulus.

The auditory streaming paradigm (van Noorden, 1975) has been extensively used to study how the human auditory system extracts coherent sound sequences (auditory streams) from a mixture of sounds emitted by concurrently active sources (cf. auditory scene analysis; Bregman, 1990). The stimulus is a repeating sound sequence of ABA-ABA-… structure, where "A" and "B" denote two sounds differing from each other in some acoustic features, such as the frequency of simple tones and "-" stands for a silent interval with the common duration of "A" and "B" (Fig. 1, top panel). Listeners can perceive this stimulus as a single stream (the integrated percept; Fig. 1, second panel), as two separate streams of isochronous sounds, one for the "A" and another for the "B" sounds (the segregated percept; Fig. 1, third panel), as well as in terms of two streams in which one stream includes some of the "A" and all of the "B" sounds while the other is made up of the rest of the "A" sounds (the combined percept; Fig. 1, fourth panel; for a full description of the variants of the combined percept, see Denham et al., 2014). The initial perception of this stimulus is strongly influenced by the stimulus parameters, with larger separation between "A" and "B" and faster presentation rates promoting the perception of the segregated and the opposite the integrated percept (for a review see Moore and Gockel, 2012). However, for longer (> 30 s) stimuli, perception inevitably switches between the alternative percepts (Anstis and Saida, 1985; Bendixen et al., 2010; Deike et al., 2012; Denham and Winkler, 2006;

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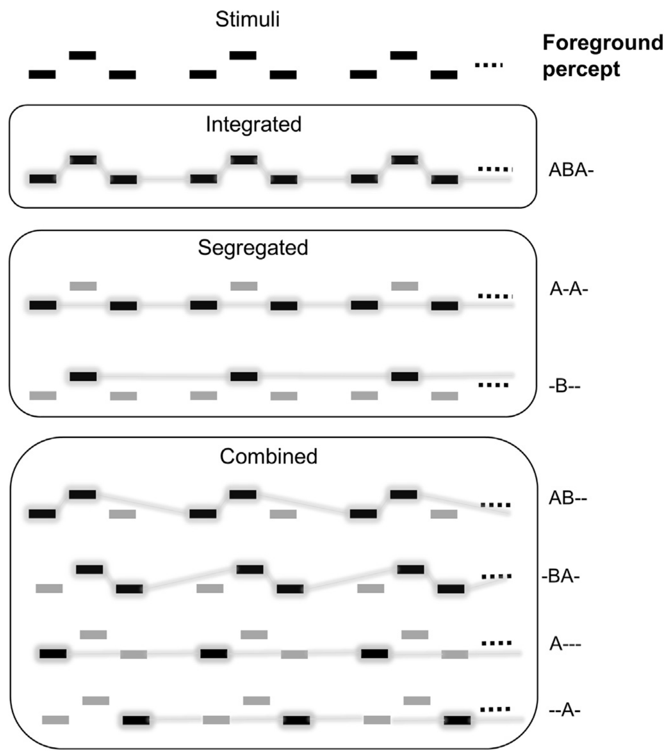

Fig. 1. Schematic depiction of the auditory streaming paradigm (top panel) and its possible perceptual interpretations grouped into 3 categories (the 3 lower panels). Rectangles depict the "A" and "B" sounds with the feature difference between them indicated by displacement in the vertical direction. Time flows along the horizontal direction. Sounds perceived as part of the same stream are connected by lines in the lower panels. Darker rectangles with grey background indicate the stream appearing in the foreground (also described with symbols to the right of each of the lower panels).

Gutschalk et al., 2005; Pressnitzer and Hupé, 2006) and the effects of the stimulus parameters are reduced at longer delays from the stimulus onset (Denham et al., 2013).

Studies using fMRI have provided information about brain regions activated during perception of the auditory streaming stimulus.[1] Auditory cortex, especially Heschl's gyrus, is more active when listeners experience the segregated than the integrated sound organization (Wilson et al., 2007). Compatible evidence was obtained with EEG by Snyder et al. (2006), who found that differences between event-related potentials elicited during integrated vs. segregated percepts probably originated from Heschl's gyrus. Deike et al. (2004) found that the left auditory cortex was more active during segregated than integrated perception of the stimulus. However, Cusack (2005) found no difference in auditory cortical activation between the two percepts; rather the intraparietal sulcus was more active during segregation than integration. The latter result is also supported by the data of Kashino et al. (2007), who found that beyond the auditory cortex, the left intraparietal sulcus, the posterior insular cortex, the supramarginal gyrus, and the thalamus were also differentially involved in the perception of the auditory streaming stimulus. These findings provide evidence that the brain network underlying auditory scene analysis extends beyond auditory cortex.

Denham et al. (2014) studied individual differences in the perception of the auditory streaming stimulus, characterizing participants' switching patterns by the conditional probabilities for transitions between perceptual alternatives (Denham et al., 2012). These authors found that although perceptual switching is stochastic, the characteristics of participants' switching patterns tended to be idiosyncratic (switching patterns from the same individual across repeated blocks were significantly more similar in comparison with those of other participants) and stable (individual similarity was preserved across sessions separated by more than a year). Farkas et al. (2016a) identified two main dimensions of the variance in individuals' switching patterns. The first one was termed *Exploration*, because individuals scoring high on this dimension experienced the least frequently reported perceptual alternative (combined) more often and the most frequently reported alternative (integrated) less often, they switched between alternatives more frequently, and required less time to discover all perceptual alternatives compared to those who scored low on the dimension. The second dimension was termed *Segregation*, because scoring high on the dimension was related to reporting more time spent experiencing the segregated and less the integrated percept (for similar dimensions found in a different group of listeners, see Kondo et al., 2017).

Ego-resiliency (ER; Block, 2002; Block and Block, 1980), a personality meta-trait of adaptive behavioral flexibility was positively linked to the *Exploration* dimension (Farkas et al., 2016a). Individuals with high ER are able to flexibly coordinate their behavior with situational demands in an adaptive way. However, Kondo et al. (2017) did not find a significant relationship between ER and idiosyncratic switching patterns in two auditory multi-stable stimulus paradigms. Discrepancies between the findings of these two studies may stem from the much larger sample size in Farkas et al. (2016a) than in Kondo et al. (2017) study ($N = 48$ and $N = 22$). Personality trait related effects typically require larger statistical power due to their higher variability. Further, Kondo et al. (2017) found that the concentration of the glutamate-glutamine (Glx) neurotransmitter measured in auditory cortex was negatively related to the *Exploration* dimension: higher Glx concentration in auditory cortex accompanied higher proportions of segregated and lower proportions of combined reports. In sum, these correlations between idiosyncratic switching patterns, individual personality traits and neurotransmitter profiles are compatible with the observed temporal stability of switching patterns, as these stable characteristics may influence the perceptual processing of multi-stable auditory stimuli. High creativity has been found to be related to increased switching in ambiguous figures (Doherty and Mair, 2012; Wiseman et al., 2011), but was found to be unrelated to individual differences in auditory streaming (Farkas et al., 2016a). However, there is a lack of consensus both in the definition (Kozbelt et al., 2010) and in the assessment (Plucker and Mackel, 2010) of creativity. Farkas et al. (2016a) study measured creativity using divergent thinking tasks (Torrence, 1988). In the current study, we decided to measure creativity using a self-report scale, as this has been found to provide a better assessment of creativity than divergent thinking tasks (Silvia et al., 2012).

In the current study, we explored the functional brain networks underlying idiosyncratic switching patterns. Functional connectivity refers to the temporal interdependence of the activity of anatomically separate brain regions. In brain networks, functionally separate regions are usually linked with each other through hubs, which integrate information from several regions (Bullmore and Sporns, 2009; Rubinov and Sporns, 2010). The low EEG frequency ranges (delta: 0–4 Hz, and theta: 4–8 Hz) are often thought to predominantly reflect long-distance connections with fewer hubs, whereas, the high frequency ranges (beta: 13–30 Hz, and gamma: 30- Hz) are indicative of short-distance connections with more hubs (Smith-Bassett and Bullmore, 2006). Graphs are used for an abstract mathematical representation of the networks. A graph is defined as a set of nodes connected with edges. The Minimum-Spanning Tree (MST) algorithm (Kruskal, 1956; Stam et al., 2014) provides a way to extract the structure of functional networks. A spanning tree is a graph that includes all nodes of the original network (N) linked by $N-1$ edges and without forming loops. MST graphs can be characterized using metrics representing the network's centrality, connectedness, and modularity.

To date, only one study has examined functional networks (though not functional connectivity in the above defined sense) in the auditory

[1] Please note that these studies only took into account the integrated and segregated perceptual alternatives.