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Neural mechanisms underlying valence inferences to sound: The role of the right angular gyrus☆

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ABSTRACT

We frequently infer others' intentions based on non-verbal auditory cues. Although the brain underpinnings of social cognition have been extensively studied, no empirical work has yet examined the impact of musical structure manipulation on the neural processing of emotional valence during mental state inferences. We used a novel sound-based theory-of-mind paradigm in which participants categorized stimuli of different sensory dissonance level in terms of positive/negative valence. Whilst consistent with previous studies which propose facilitated encoding of consonances, our results demonstrated that distinct levels of consonance/dissonance elicited differential influences on the right angular gyrus, an area implicated in mental state attribution and attention reorienting processes. Functional and effective connectivity analyses further showed that consonances modulated a specific inhibitory interaction from associative memory to mental state attribution substrates. Following evidence suggesting that individuals with autism may process social affective cues differently, we assessed the relationship between participants' task performance and self-reported autistic traits in clinically typical adults. Higher scores on the social cognition scales of the AQ were associated with deficits in recognising positive valence in consonant sound cues. These findings are discussed with respect to Bayesian perspectives on autistic perception, which highlight a functional failure to optimize precision in relation to prior beliefs.

1. Introduction

To navigate the social environment, humans rely on their capacity to recognise cues signalling potentially threatening or affiliative value in others' mental states. The present study builds upon knowledge derived from music perception to elucidate cognitive mechanisms and neural systems involved in this ability.

The proposition that pleasant-sounding (consonant) combinations of tones entail special numerical properties has been ascribed to Pythagoras (Apel, 1972). He is supposed to have observed that tones produced by partitioning a vibrating string in two segments with lengths related by simple (i.e. small-integer) ratios, such as 2:1, 3:2 and 4:3, resulted in more pleasing harmonies compared to those produced by more complex ratios (e.g. 9:8, 16:15). Empirical evidence from studies conducted with infants, children, and adults, indeed suggests that sequential pure-tone intervals with simple frequency ratios confer perceptual processing advantages (Schellenberg and Trehub, 1994, 1996a, 1996b). Researchers have argued that intervals with simple ratios would be inherently easier to encode, manage and recognise as a unit (i.e. more coherent: Frances, 1972; Bharucha and Pryor, 1986) forming prototypes (Rosch, 1975) that would provide a perceptual frame of reference for distinguishing other intervals (Trehub and Unyk, 1991). It has been proposed that the special perceptual status of intervals with simple frequency ratios, such as the octave (2:1), perfect fifth (3:2), and perfect fourth (4:3), could stem from their presence in naturally occurring sounds including those of speech and music (Terhardt, 1978, 1984), or that it may result from the exposure to particular musical cultures or styles (Serafine, 1983; Dowling and Harwood, 1986). Such distinctiveness has also been reflected in judgments of consonance and dissonance; with simple-ratio intervals being judged more consonant (i.e. more pleasant, smooth and well blended) than intervals with more complex ratios, such as the major second (9:8), minor second (16:15), and tritone (45:32), which have been consistently evaluated as more dissonant (i.e. more unpleasant and less

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smooth) (Schellenberg and Trehub, 1994; Plomp and Levelt, 1965; Wedin, 1972; Zentner and Kagan, 1996; Schellenberg and Trainor, 1996; Trainor and Heinmiller, 1998; Blood et al., 1999).

The present study focuses on the emotional effects and, in particular, on the valence judgments elicited by musical intervals of different degrees of consonance/dissonance. There is substantial evidence showing that level of consonance/dissonance is strongly associated with the percept of valence (Blood et al., 1999; Costa et al., 2000; Plomp and Levelt, 1965; Trainor and Heinmiller, 1998). Valence has been defined as the subjective feeling of pleasantness or unpleasantness (Barrett and Wager, 2006; Lindquist et al., 2012; Russell, 1979). With regards to social interaction, valence has been conceptualized as the intrinsic attractiveness/good-ness (positive valence) or averseness/badness (negative valence) of an event, object or situation (Colombetti, 2005; Frijda, 1986). Together with arousal and potency, they have been proposed as the three affective dimensions widely considered to explain the fundamental variance of emotional responses (Lang et al., 1993; Russell, 1979). Researchers have frequently utilised the valence percept as an indirect measure to assess degree of consonance/dissonance (Blood et al., 1999; Gosselin et al., 2006; Koelsch et al., 2006; Plomp and Levelt, 1965; Trainor and Heinmiller, 1998). Valence inferences have been shown to consistently index the perception of consonance/dissonance level in Western musicians and non-musicians (Blood et al., 1999; Bugg, 1970; Plomp and Levelt, 1965) and an association between valence and degree of dissonance has been also reported in listeners never exposed to Western music (Fritz et al., 2009). Although the affective appraisal of musical dissonance seems to be strongly influenced by culture, as demonstrated by studies that have documented its variations across different cultures and its historical transformation through distinct Western culture periods (Burns, 1999), valence judgments applied to stimuli with distinct degrees of sensory dissonance (the type of dissonance manipulated in the present study) appear to be culturally invariant and largely independent of musical training [(Bidelman and Krishnan, 2011; Chiandetti and Vallortigara, 2011; Fannin and Braud, 1971; Foss et al., 2007; Fujisawa and Cook, 2011; Itoh et al., 2010; Izumi, 2000; Minati et al., 2009; Peretz et al., 2001; Sugimoto et al., 2010; Zentner and Kagan, 1996) although see also: (McDermott and Hauser, 2004; McDermott et al., 2016)].

Various psychoacoustic models have been suggested to elucidate why musical intervals comprising simple frequency ratios are experienced as more consonant than intervals involving complex ratios (Helmholtz and Ellis, 1895; Kameoka and Kuriyagawa, 1969; Plomp and Levelt, 1965; Terhardt, 1978). One influential theory was coined by Helmholtz (1895), who proposed that sensory consonance/dissonance was related to the absence/presence of interactions (sensation of "beats" or "roughness") between the harmonic spectra of two pitches. Empirical evidence has also shown that the perception of consonance/dissonance can be elicited not only by the properties of a single signal, such as roughness, but also when tones are presented dichotically (i.e. when different pitches are presented separately to each ear) (Cousineau et al., 2012; Fritz et al., 2013; McDermott et al., 2010). Fritz and collaborators (2013) have shown that dichotic dissonance stimulation also elicits negative valence ratings, which indicates that cochlear interactions may not be critical for the perception of dissonance. It is important to note, however, that during dichotic listening tasks, the allocation of attention in the auditory space can be modulated by training (Soveri et al., 2013) and, consequently, participants' valence judgments during dichotic paradigms could also be explained by attentional focus on one ear. To overcome this potential problem, in the present work we employed sequential intervals presented diotically (each tone was audible by both ears simultaneously), which do not produce roughness or beats due to their non-simultaneity; yet sequential intervals are also known to be judged along the dimension of consonance/dissonance according to their frequency ratios (Ayres et al., 1980; Fritz et al., 2013; Schellenberg and Trehub, 1994).

Several studies have investigated the neural correlates of emotional responses to dissonance. Five relevant neuroscientific studies should be mentioned. The study by Blood and collaborators (1999) used positron emission tomography (PET) to measure the brain correlates of negative affective reactions induced by dissonance. Degree of dissonance was controlled by presenting participants with a novel melody, which was manipulated through altering the harmonic structure of its accompanying chords. A preliminary behavioural study showed that higher levels of dissonance were correlated with higher average ratings of adjectives associated with negative emotions (e.g. tense, unpleasant, irritated, annoying, dissonant and angry). Participants were informed that the experimenters were interested in their emotional responses to music, and they were asked to respond to an emotional discrimination task (rating emotional valence). Increasing dissonance correlated with activity in right parahippocampal gyrus and right precuneus. Higher ratings of unpleasantness, which correlated with increasing dissonance, covaried with cerebral blood flow changes in right parahippocampal gyrus and left posterior cingulate. On the other hand, activations in orbitofrontal, subcallosal cingulate and frontal polar cortex correlated with decreasing dissonance (equivalent to increasing consonance). Koelsch et al. (2006) used fMRI to investigate the brain circuits mediating emotions with positive and negative valence elicited by consonant and permanently dissonant counterparts of the original tunes (classical music from the common practice period). In contrast to the study by Blood et al. (1999), which used musical stimuli presented via computerized control and without musical expression, they employed naturalistic music taken from commercially available CDs. The unpleasant stimuli were obtained by electronically manipulating "joyful" naturalistic instrumental dance-tunes ('the original -pleasant- excerpt was recorded simultaneously with two pitch shifted versions of the same excerpt, the pitch-shifted versions being one tone above and a tritone below the original pitch'). Participants had to indicate how pleasant or unpleasant they felt following each musical excerpt. During the presentation of unpleasant music (contrasted to pleasant music), activations were found in the left hippocampus, the left parahippocampal gyrus, the right temporal pole, and the left amygdala. When contrasting pleasant vs. unpleasant music, they observed activations of Heschl's gyrus, the anterior superior insula, and the left inferior frontal gyrus. In the study by Gosselin et al. (2006), a group of epileptic patients with anteromedial lobe excision were examined (brain regions removed included variable amounts of parahippocampal, perihinal, entorhinal and hippocampal tissue). Patients were asked to rate the degree of pleasantness of consonant and dissonant manipulated versions of the same happy or sad musical excerpts. They noticed that patients with parahippocampal resection showed diminished sensitivity to unpleasant (dissonant) music, judging the dissonant stimuli as moderately pleasant (significantly happier compared to normal controls). The authors interpreted the contribution of the parahippocampal cortex as 'specific to the emotional interpretation of dissonance'. A fourth relevant study, conducted by Green et al. (2008), which was aimed at exploring brain activity underlying musical mode perception, found increased activity in the left parahippocampal gyrus, bilateral ventral anterior cingulate cortex and left medial prefrontal cortex in response to minor mode melodies, compared to equivalent major melodies. The authors proposed harmonic dissonance as a possible contributing factor in the observed minor related activity increase. Finally, also using fMRI Foss et al. (2007) found that the anterior cingulate cortex, inferior frontal gyrus, superior temporal gyrus, medial frontal gyrus and inferior parietal lobule responded to increasing dissonance with progressively more activation.

Although the findings of these studies only partially overlap (and in some cases contradict each other), they converge in supporting a critical role of the parahippocampal cortex and, to a less extent, of medial prefrontal cortices (e.g. anterior cingulate cortex and medial prefrontal cortex) in the emotional evaluation of perceived degrees of dissonance (Blood et al., 1999; Foss et al., 2007; Gosselin et al., 2006; Green et al., 2008; Koelsch et al., 2006).