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CHAPTER

21 Neural Mechanisms of Musical Imagery 3

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Abstract

Findings regarding the neural mechanisms of musical imagery are summarized, and both auditory and motor components of musical imagery are considered. Similarities of musical imagery and music perception (involving results from studies using behavioral and psychophysical methods, clinical data from brain-damaged patients, electrophysiology, and brain imaging), examples of involuntary musical imagery (involving anticipatory musical imagery, musical hallucinations, schizophrenia, earworms, and synesthesia), and aspects of embodied aspects of musical imagery (involving spatial and force metaphors, mimicry, the inner ear/inner voice distinction, effects of mental practice and performance, dance and other motor acts, and musical affect) are considered. It is concluded that many neural mechanisms involved in musical imagery are similar to neural mechanisms involved in music perception, cognition, and production. The importance of motor activation to musical imagery is highlighted, and the importance of an embodied approach to musical imagery is discussed.

Keywords: musical imagery, inner ear and inner voice, earworms, musical hallucinations, mental practice,

embodied cognition

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IN the early years of the cognitive approach to psychology, cognitive processes were considered analogous to software and the brain was considered analogous to hardware. Software and hardware can be viewed as relatively independent, and so there was not much focus on the neural mechanisms of cognitive processes. However, with the development of brain imaging technologies that allowed examination of functioning in intact living brains, researchers began to make significant advances in linking different cognitive processes with different neural mechanisms, and questions about the neural mechanisms of cognition became more central. Music offered an excellent venue for investigation of neural mechanisms of cognition (e.g., Peretz & Zatorre, 2003) and brain plasticity (e.g., Herholz & Zatorre, 2012; Schlaug, 2015). The importance of understanding neural mechanisms of cognition was underscored by the emergence of the notion of embodied cognition, an approach which suggests that cognitive functioning is influenced by characteristics and properties of embodied experience (e.g., Barsalou, 2008; Gibbs, 2005; Shapiro, 2010; Wilson, 2002). Indeed, there have recently been calls for an embodied cognition approach to the study of music (e.g., Cox, 2016). Most papers in psychology and neuroscience of music focused on perception, cognition, and performance (e.g., Levitin & Tirovolas, 2009), and there has been less focus on musical imagery. This chapter will focus on neural mechanisms of musical imagery across a range of domains.

Music is generally considered an auditory stimulus, but perceptual and cognitive representation of music can involve non-auditory (e.g., kinesthetic) information, and musical imagery involves auditory and nonauditory components. Studies involving auditory and non-auditory components of musical imagery and that have implications for understanding neural mechanisms of musical imagery are considered. Studies involving only behavioral or psychophysical measures of musical imagery are reviewed in Hubbard 🖟 (2010, 2013a, 2013b, 2018, forthcoming) and are not considered here unless those studies have implications for understanding neural mechanisms of musical imagery. Studies involving neuroscience of music that do not generate testable predictions regarding musical imagery are also not considered here. The similarity of imagery and perception of musical stimuli is addressed, and results from studies involving behavioral and psychophysical methods, clinical studies of brain-damaged individuals, and physiological data involving electrophysiology and brain imaging are considered. Involuntary musical imagery is addressed, and examples involving anticipatory musical imagery, musical hallucinations, musical imagery accompanying schizophrenia, earworms, and the relative lack of musical imagery in synesthesia are considered. Embodied musical imagery is addressed, and examples involving spatial and force metaphors, the role of mimicry, the distinction between the inner ear and inner voice, the effects of mental practice on performance, musical imagery and dance, and musical affect are considered. A brief summary and conclusions are then presented.

Imagery and Perception of Music

Imagery often seems to exhibit perception-like qualities, and a starting point for many studies of musical imagery involves the similarity of imagery and perception. There have been three main approaches to examining the relationship between imagery and perception, and these involve (a) behavioral and psychophysical studies; (b) studies of patients with brain damage; and (c) brain-imaging methods such as electroencephalography (EEG), positron emission tomography (PET), and functional magnetic resonance imaging (fMRI).

Behavioral and Psychophysical

There are many similarities in behavioral and psychophysical data regarding musical imagery and music perception. Properties of perceived and imaged musical tones such as pitch (Hubbard & Stoeckig, 1988) and timbre (Crowder, 1989) prime subsequently perceived tones with matching properties. Imaged tempo for a familiar tune matches the typical performance tempo for that tune (Halpern, 1988b; Jakubowski, Farrugia, & Stewart, 2016), and studies in which participants scanned through an imaged melody found that relative latencies between notes are preserved (e.g., Halpern, 1988a; Zatorre, Halpern, & Bouffard, 2010; Zatorre, Halpern, Perry, Meyer, & Evans, 1996). Musical images preserve harmonic relatedness and tonality (Hubbard & Stoeckig, 1988; Vuvan & Schmuckler, 2011) and exhibit a weak form of absolute pitch (Halpern, 1989; Schellenberg & Trehub, 2003). Pitch acuity is similar in perceived and imaged musical pitch, but temporal acuity is worse in musical imagery than in perception (Janata & Paroo, 2006). Not surprisingly, pitch acuity in imagery is better in participants with more musical training (Cebrian & Janata, 2010b). p. 523 Right-handed experimental participants instructed to image 👃 a voice often localize that voice on their right side (Prete, Marzoli, Brancucci, & Tommasi, 2016), consistent with the right ear advantage for speech, and it could be hypothesized that side preferences found in music perception should be found for musical imagery. In general, findings are consistent with hypotheses that musical imagery preserves structural and temporal properties of a musical stimulus and that imagery of musical stimuli involves many of the same neural mechanisms as music perception.

Brain Damage

Although there have been numerous studies of the effects of brain damage on music perception, cognition, and production (for reviews, see Marin & Perry, 1999; Peretz & Zatorre, 2005; Stewart, von Kriegstein, Warren, & Griffiths, 2006), there have been relatively few studies of musical imagery in patients with brain damage. The studies that have been reported typically compared performance involving imagery in braindamaged patients with performance on the same task in a control group. Patients with damage to the right temporal lobe performed worse on pitch comparisons in imagery and in perception than did patients with damage to the left temporal lobe or control participants (Zatorre & Halpern 1993). Halpern (2003) suggested these lesion data and subsequent imaging data (from Zatorre et al., 1996) demonstrated the right superior temporal gyrus is involved in comparisons of pitch in imagery (see also Samsom & Zatorre, 1991). Patients with right temporal lobe damage to the area including Heschl's gyrus do not perceive a missing fundamental (Zatorre, 1988), and this is consistent with a role for this area in top-down representation of pitch. Patients with right hemisphere damage have difficulty in processing information regarding musical interval and musical contour (Liégois-Chauvel, Peretz, Babaï, Laguitton, & Chauvel, 1998; Peretz, 1990) and in identification of sad music (Khalfa, Schon, Anton, & Liégeois-Chauvel, 2005), and this predicts such patients would have similar difficulties in musical imagery. More positively, music influences brain plasticity, and so it could be predicted that musical imagery might be useful in the treatment of some neurological damage or disorders (e.g., melodic intonation therapy, Peretz, 2013; also Bringas et al., 2015; Sabaté, Llanos, & Rodriguez, 2008; Särkämö, Altenmüller, Rodriguez-Fornells, & Peretz, 2016).

Clinical studies of individuals with trauma-induced amusia (e.g., Marin & Perry, 1999; Satoh, 2014) or congenital amusia (e.g., Peretz, 2013) have shed light on neural mechanisms of music processing, but musical imagery has typically not been studied in such individuals. Amusias might have a basis in perception or memory (Peretz, 2002); to the extent an amusia involves dysfunction of memory, imagery might be impacted (e.g., Satoh, 2014, explicitly identifies memory as internal imagery), but to the extent an amusia involves dysfunction in perception, imagery might be relatively spared. Also, parallels between types of amusia and types of aphasia (e.g., receptive, production) suggest there may be some overlap in neural mechanisms that process music and neural mechanisms that process language (cf. Besson & Schön, 2003; Marin & Perry, 1999; Patel, 2008). Additionally, findings that patients with amusia have difficulty in

spatial tasks such as 4 mental rotation (Douglas & Bilkey, 2007; but see Tillmann et al., 2010), coupled with findings that some types of musical imagery manipulation involve cortical areas implicated in mental rotation (Zatorre et al., 2010), suggest such patients might have impaired musical imagery. Studies of patients with amusia suggest music functions are not as strongly lateralized as language functions (Alossa & Castelli, 2009), and this has been confirmed in non-patient studies as well (e.g., Parsons, 2003; Platel et al., 1997). Also, presence of amusia predicts deficits in auditory emotion recognition in schizophrenia, and this might reflect development of music and language from the same musical protolanguage (Kantrowitz et al., 2014).

Physiological Measures

Many studies recorded physiological measures in an attempt to understand neural mechanisms of musical imagery. These studies typically involved electrophysiology such as EEG and event-related potential (ERP) or brain imaging such as PET and fMRI (for review, see Koelsch, 2012).

Electrophysiology

Imaging a melody results in more high-band synchronized alpha than does perceiving a melody (Schaefer, Vlek, & Desain, 2011; Villena-González, López, & Rodríguez, 2016), and alpha is increased during imagery of more complex tones (van Dijk, Nieuwenhuis, & Jensen, 2010). Emitted potentials occur when a musical note is expected but not presented (Cebrian & Janata, 2010b; Janata, 2001), and these are similar to evoked potentials elicited by presentation of a musical note. There are differences in size of the N1 in response to a perceived tone as a function of image accuracy and whether preceding tones were imaged or perceived (Cebrian & Janata, 2010a). If a participant deliberately generates an auditory image appropriate to a stimulus seen in a visual picture, P2 and LPC are increased (Wu, Mai, Chan, Zheng, & Luo, 2006). A larger mismatch in loudness or pitch between imaged tones and subsequent perceived tones elicits a larger N2 (Wu, Mai, Yu, Qin, & Luo, 2010) and lower-pitched or louder images and percepts evoke a larger N1 and LPC (Wu, Yu, Mai, Wei, & Luo, 2011). Accented beats in a sequence of imaged or perceived beats result in a larger positive amplitude after 180-250 milliseconds and a larger negative amplitude after 350 milliseconds (Vlek, Schaefer, Gielen, Farquhar, & Desain, 2011). Relatedly, rhythmic aspects of melody are more easily isolated in EEG than are pitch or melody-driven aspects (Schaefer, Desain, & Suppes, 2009). Mismatch negativity is evoked in musicians for perceived and for imaged musical stimuli (Herholz, Lappe, Knief, & Pantev, 2008; Yumoto et al., 2005). Continuation of a lyric in imagery during an unexpected silent gap in familiar music results in several changes in perceptual, attentional, and cognitive components of ERPs (Gabriel et al., 2016). In highly trained musicians, ERPs while reading a visual musical score are indistinguishable from ERPs while listening to auditory notes (Simoens & Tervaniemi, 2013). In general, imagery of a musical stimulus results in generation of ERP or EEG patterns similar to those generated by perception of a musical stimulus.

p. 525 Brain Imaging

There have been numerous studies involving brain imaging during processing of musical stimuli (for reviews, see Koelsch, 2010, 2012; also Peretz & Zatorre, 2003) and changes in the brain related to musical training (Wan & Schlaug, 2013). There is substantial overlap of cortical areas activated in musical imagery and activated in music perception, especially in Wernicke's area and its right hemisphere homologue (Zhang, Chen, Wen, Lu, & Liu, 2017) and auditory association areas (e.g., Daselaar, Porat, Huijbers, & Pennartz, 2010; Herholz, Halpern, & Zatorre, 2012; Zatorre et al., 1996). Spontaneous imagery during an unexpected gap in a well-known musical piece (Kraemer, Macrae, Green, & Kelley, 2005) or during a silent gap prior to the start of an expected music track on a familiar CD (Leaver, van Lare, Zielinski, Halpern, & Rauschecker, 2009) involves activation of auditory association areas as well as prefrontal and motor areas. Auditory imagery may activate frequency-specific regions in primary auditory cortex (Oh, Kwon, Yang, & Jeong, 2013). When participants listen to four-part harmony, there is greater activation in bilateral temporal lobes, cingulate gyrus, and medial cerebellum when participants focus on the harmony as a whole, but greater activation of superior parietal, bilateral precuneus, and bilateral orbital frontal cortices if participants focus on a particular (e.g., alto) line (Satoh, Takeda, Nagata, Hatazawa, & Kuzuhara, 2001). Judgment of similarities of perceived timbres and of imaged timbres results in similar cortical activation (Halpern, Zatorre, Bouffard, & Johnson, 2004): secondary auditory cortex and supplementary motor cortex are activated in both imagery and perception, but primary auditory cortex is activated only in perception (see also Zhang et al., 2017). Indeed, passive listening to music by musicians (Haueisen & Knösche, 2001) and non-musicians (Perrone-Capano, Volpicelli, & di Porzio, 2017) who remain motionless results in activation of cortical motor areas.

Participants who self-report more vivid musical imagery exhibit greater activation in right superior temporal gyrus and prefrontal cortex (Herholz et al., 2012) and in right parietal cortex (Zatorre et al., 2010). Higher self-reported vividness of auditory imagery correlates with gray matter volume in left inferior parietal lobe, medial superior frontal gyrus, middle frontal gyrus, and left supplementary motor area (Lima et al., 2015). Application of TMS over the right hemisphere (to disrupt cortical activation) disrupts pitch discrimination (Halpern, 2003). Imagery reversal of a musical stimulus (i.e., scanning backward through a melody; Zatorre et al., 2010) activates intraparietal sulcus and ventrolateral and dorsolateral frontal cortex (areas involved in manipulating sensory information). Musicians who read a musical score initially exhibit activation in occipital areas that spreads to midline parietal and then to left temporal auditory association areas and right premotor areas, and this pattern could reflect emergence of notational audiation, that is, auditory imagery of a piece of music that is evoked by reading the musical score of that piece (Schürmann, Raij, Fujiki, & Hari, 2002). Participants instructed to image a single note exhibit activation of bilateral superior temporal gyri, medial and inferior frontal gyri, and precuneus (Yoo, Lee, & Choi, 2001). Overall, brain imaging studies generally support the idea that neural mechanisms are shared between imagery and perception and between imagery and production (see later subsection on "Mental 4 Practice and Performance"), although there are exceptions (e.g., primary auditory cortex is less likely to be activated during imagery than during perception).

Involuntary Musical Imagery

The majority of laboratory studies of musical imagery involve images created in response to a stimulus or task demand, and as noted above, these studies suggest such imagery generally recruits neural mechanisms similar to those used in music perception, cognition, and performance. However, musical imagery can be involuntary and occur spontaneously and without conscious control. Five types of involuntary musical imagery are considered here, namely (a) anticipatory musical imagery, (b) musical hallucinations, (c) musical imagery in schizophrenia, (d) earworms, and (e) synesthesia.

Anticipatory Musical Imagery

Involuntary musical imagery reflects anticipation of an upcoming or ongoing musical stimulus. As noted earlier, when participants encounter an unexpected silent gap when listening to a familiar melody, they often report continuation of the melody in imagery; such continuation is linked with activation in auditory association areas and, when linguistic information (e.g., lyrics) isn't available, in primary auditory cortex (Kraemer et al., 2005). Similarly, listeners who expect a musical stimulus but are presented with silence exhibit emitted potentials similar to the evoked potentials that occur when a musical stimulus is perceived (Janata, 2001). As noted earlier, when listening to a familiar CD, participants often experience mental imagery of an upcoming track during the silent period before that track; such imagery is linked with activity in rostral prefrontal cortex and motor areas (Leaver et al., 2009). Notational audiation can be considered anticipatory musical imagery, as content of audiation anticipates what would be heard if the notated music was performed. Indeed, ERPs in highly trained musicians during visual note reading are indistinguishable from ERPs during auditory note perception (Simoens & Tervaniemi, 2013). The existence of anticipatory musical imagery is consistent with hypotheses that imagery is an internal predictive process (e.g., Neisser, 1976; Tian & Poepple, 2012) and that anticipatory musical imagery might be linked with expectations that contribute to musical affect (cf. Huron, 2006; Juslin & Västfjäll, 2008).

Musical Hallucinations

In voluntary musical imagery, individuals have volitional control over imagery and are aware that the sound does not emanate from a stimulus in the environment. In musical hallucinations, there is no volitional control over imagery and sounds are perceived to 4 emanate from objects in the environment. Musical hallucinations are classified as idiopathic if they occur in the absence of associated psychopathology (other than hearing impairment) and as sympathetic if they are associated with concurrent psychopathology such as depression or schizophrenia (Coebergh, Lauw, Bots, Sommer, & Blom, 2015). Common etiological factors for musical hallucinations are brain injury, epilepsy, psychiatric disorder, and intoxication/pharmacology (Evers, 2006; Evers & Ellger, 2004). Musical hallucinations can accompany hearing loss (e.g., Hammeke, McQuillen, & Cohen, 1983), possibly because lack of auditory input disinhibits cortical mechanisms of auditory imagery and perception (Griffiths, 2000). Patients with hearing loss might experience musical imagery rather than other types of auditory imagery because music is more predictable and repetitive than are other types of auditory stimuli (Kumar et al., 2014). Dysfunction of temporal cortex (e.g., Kasai, Asada, Yumoto, Takeya, & Matsuda, 1999), right hemisphere focal brain lesions (Berrios, 1991; but see Keshavan, Davis, Steingard, & Lishman, 1992; Kumar et al., 2014), and activity in right superior temporal gyrus (Penfield & Perot, 1963), posterior middle right temporal lobe (Griffiths, Jackson, Spillane, Friston, & Frackowiak, 1997), superior temporal sulcus (Bernardini, Attademo, Blackmon, & Devinsky, 2017), and cerebellum (Griffiths, 2000) are linked to the presence of musical hallucinations. However, given that cerebral localization of music processing is dependent upon musical background and experience, the relationship between neural mechanisms and musical hallucinations could exhibit significant individual differences.

Schizophrenia

The most commonly investigated psychopathology within auditory imagery literature is schizophrenia. Although the majority of investigations of schizophrenia focused on auditory hallucinations involving verbal stimuli (e.g., Cho & Wu, 2013; Evans, McGuire, & David, 2000; Johns et al., 2001; McGuire et al., 1996; Shergill, Bullmore, Simmons, Murray, & McGuire, 2000), cases of musical hallucinations have been documented. Saba and Keshavan (1997) documented sixteen patients with schizophrenia who reported musical hallucinations. Musical imagery in schizophrenia is typically hallucinatory (not under voluntary control), and Baba and colleagues (Baba, Hamada, & Koca, 2003) suggested a model of musical hallucination in schizophrenia in which musical imagery becomes more obsessive in quality, is perceived as originating outside the individual, and is ultimately accepted as part of the self. The content of musical hallucinations in schizophrenia is often described as religious, and this is consistent with observations that delusions in schizophrenia often contain religious themes (e.g., Galant-Swafford & Bota, 2015). Brain imaging acquired during a schizophrenic patient's musical hallucinations revealed increased activity in right orbitofrontal cortex (Bleich-Cohen, Hendler, Pashinian, Faragian, & Poyurovsky, 2011). Relatedly, differences in brain activation patterns of patients with schizophrenia and controls when spoken sentences were imaged in another person's voice, but not when sentences were imaged in the participant's own 4 voice (McGuire et al., 1995), suggest articulatory information relative to the inner voice (discussed later in the chapter) might be overly represented in schizophrenia.

Earworms

Perhaps the fastest growing area of research on musical imagery during the past several years involves earworms (also referred to as involuntary musical imagery, stuck-song syndrome, brain worms, sticky music, intrusive musical imagery, and perpetual music track; see Williams, 2015). Earworms are a fragment of a song or melody that repeatedly and involuntarily occupies an individual's awareness. Unlike musical hallucinations, earworms are generally not considered to reflect psychopathology and are usually not considered distressing by those who experience them (Beaty et al., 2013; Halpern & Bartlett, 2011; Hemming & Merrill, 2015). Research on earworms has focused on descriptive phenomenology and behavioral correlates (for summary, see Hubbard, forthcoming), and there has been little consideration of neural mechanisms of earworms. Levitin (2007) suggested earworms occur when neural areas representing a specific piece of music get stuck in "playback mode." Farrugia and colleagues (Farrugia, Jakubowski, Cusack, & Stewart, 2015) found that frequency of occurrence of earworms was related to cortical thickness in the right frontal and temporal cortices and anterior cingulate, whereas affective aspects of involuntary musical imagery were related to gray matter volume in right temporopolar and parahippocampal cortices. It could be predicted that neural mechanisms previously shown to be involved in voluntary musical imagery might be activated during earworms, and there might be additional (or lack of) activation in other areas or differences in time course of activation that reflect the involuntary nature of earworms (e.g., differences in voluntary voice imagery and involuntary voice hallucinations; Linden et al., 2011).

Synesthesia

Synesthesia occurs if a stimulus in one dimension or modality induces systematic and idiosyncratic perceptual experience of a specific stimulus in a different dimension or modality (e.g., hearing a specific sound induces visual experience of a specific color, e.g., Baron-Cohen & Harrison, 1997; Cytowic, 2002; Robertson & Sagiv, 2005). Reports of synesthesia in which a non-musical stimulus elicits musical imagery are rare (e.g., see listings in Cytowic & Eagleman, 2011; Day, 2016), and perhaps the most well-known is that of composer Jean Sibelius, who experienced different musical chords when viewing different colors (Pearce, neither musical hallucinations nor earworms match the typical phenomenology of synesthesia (e.g., specific synesthetic experiences are evoked by specific stimuli and consistent over long periods of time). Most research on neural mechanisms of synesthesia focused on color-grapheme synesthesia (in which perception of letters or numerals induced experience of color; e.g., Rouw & Scholte, 2010), and there has been little research involving neural mechanisms of synesthesia involving musical imagery. Possible neural mechanisms of synesthesia involve activation (Ramachandran & Hubbard, 2001) or disinhibition (e.g., Grossenbacher & Lovelace, 2001) of cross-connections between sensory areas, and so one speculative possibility is that lack of evoked musical imagery in synesthesia might be related to the general lack of activation in primary auditory cortex during musical imagery. Another speculative possibility is that musical perception already involves non-auditory (e.g., kinesthetic) elements, and so activation of other non-auditory information in musical imagery is not experienced as synesthesia per se.

Embodied Musical Imagery

Explanations of musical phenomena that are based on properties of the human body have a long history (e.g., dissonance and consonance reflect beat interference along the basilar membrane; Greenwood, 1961; see also Hodges, 2009). However, recent developments in cognitive science suggest characteristics of embodied experience more actively influence perception, cognition, and action (e.g., motor theory of speech perception, Liberman & Mattingly, 1985; mirror neurons, Iacoboni, 2009; Oztop, Kawato, & Arbib, 2006). Indeed, observations that music spontaneously engages our bodies in multiple ways (e.g., tapping along with a beat, attributing an accent pattern to isochronous beats) suggest music offers a promising venue in which to investigate embodied cognition (e.g., see Reybrouck, 2001). Aspects of embodiment that are relevant to musical imagery include (a) spatial and force metaphors, (b) use of mimicry, (c) the inner ear and inner voice distinction, (d) mental practice and performance, (e) the relationship between music and dance, and (f) musical affect.

Spatial and Force Metaphors

Much of human cognition is based on metaphor (Lakoff & Johnson, 1980), and many prevalent metaphors reflect properties of embodiment and might influence image 4 schemata (including motor imagery) and other aspects of cognition (Lakoff & Johnson, 1999). One example involves the notion of pitch height (for discussion, see Cox, 2016). Faster auditory frequencies are judged to be "higher" in pitch than are slower auditory frequencies, and responding to stimuli in specific spatial locations is usually improved when visual stimuli higher in the picture plane are associated with faster auditory frequencies (Deroy, Fernandez-Prieto, Navarra, & Spence, 2018; Elkin & Leuthold, 2011; Keller, Dalla Bella, & Koch, 2010). Related to pitch height are notions that a sequence of notes forms a contour and that melody moves in steps and leaps such that notes successive in time are represented as motion in space (Johnson & Larson, 2003). More broadly, Larson (2012) suggested analogues of physical inertia, gravitational attraction, and magnetism occur in music, and Hubbard (2017) addressed the possibility of an analogue of momentum in music. Eitan and Granot (2006; Eitan & Timmers, 2010) identify many motion metaphors in musical space (e.g., crescendo is associated with approach and with acceleration). Neural mechanisms of spatial and force metaphors have not received extensive research, although it could be predicted that cortical areas involved in processing motion information could be activated (e.g., much as a still photograph depicting a specific direction of motion activates cortical motion processing areas; e.g., Senior et al., 2000; Senior, Ward, & David, 2002) in both music perception and musical imagery.

Mimicry

Listening to or recalling music has been suggested to involve motor mimicry (Cox, 2016). Many musical sounds provide information regarding the human motor action that produced those sounds (including information involving spatial and force metaphors), and musical imagery is often accompanied by visual or motor images related to the sound source (Godøy, 2001). Cox suggested an important component of music comprehension is imitating, either overtly or covertly, the sound-producing actions of performers. Such imitative movements might involve movements appropriate to playing an instrument or subvocal imitation of musical sounds, and musical features (e.g., pitch, duration, strength, etc.) might be represented mimetically; indeed, even simple tapping along with the beat might be considered mimicry. Western popular music has been dominated by music that is easily singable or danceable (Cox, 2016), and this is consistent with the importance of embodiment and mimicry in music processing. Such mimicry might involve overt physical action or covert firing of mirror neurons. Mirror neurons can be activated by sounds associated with a given action (Kohler et al., 2002), and so might be involved in neural activity relevant to singing or playing an instrument. One consequence of such mimicry is that musical imagery involves kinesthetic and proprioceptive information (Hubbard, 2013b), and the importance of kinesthetic and proprioceptive information in auditory and musical imagery is seen in the distinction between the inner ear and inner voice and in separate roles of auditory imagery and kinesthetic imagery in mental practice and performance.

p. 531 Inner Ear and Inner Voice

In addition to perceiving sounds generated by stimuli in the environment, humans perceive sounds they generate with their bodies, most commonly vocalizations (e.g., speaking, singing). Just as listening to external sounds or generating vocalizations involve the ear or the voice, respectively, auditory imagery of external sound or vocalization has been hypothesized to involve the "inner ear" or "inner voice," respectively (see Hubbard, 2010, 2013b). A distinction between the inner ear and inner voice underscores one way in which musical imagery (and auditory imagery in general) reflects embodied experience, as elements of the inner voice are linked to articulatory gestures involved in speech, singing, or other sound production. The distinction between the inner ear and inner voice is often related to Baddeley's model of working memory (Baddeley, 1986, 2000), which contains a phonological store used for retention of auditory material and an articulatory rehearsal mechanism that recodes stimuli for the phonological store. More specifically, the inner ear is linked to a passive phonological store and the inner voice is linked to a more active articulatory rehearsal mechanism. Evidence for the existence of such separate processes is based on a variety of findings (see Hubbard, 2010, 2013b, 2018, forthcoming). Just as the phonological store and articulatory rehearsal mechanism are separate structures or processes that generally work together but can be experimentally separated, Smith and colleagues (Smith, Wilson, & Reisberg, 1995) suggested the inner voice and inner ear are separate structures or processes that generally work together but can be experimentally separated.

Activation of motor areas in musical and auditory imagery has been found in multiple studies (for review, see Lima, Krishnan, & Scott, 2016; Zatorre & Halpern, 2005). Consistent with this, if participants cannot subvocalize during an experimental task involving auditory imagery, thus interfering with potential articulatory activity, performance on some tasks involving auditory imagery is affected (e.g., Reisberg, Smith, Baxter, & Sonenshine, 1989; Smith et al., 1995); this suggests motor activity in the form of articulatory gestures influences at least some auditory imagery (see also Aleman & van't Wout, 2004). When tasks specified by Smith et al. (1995) to utilize the inner ear or inner voice were given to schizophrenia patients, there were no differences in performance (Evans et al., 2000), and this is consistent with confusion of self-generated and other-generated vocalization in schizophrenia. Studies of Halpern, Zatorre, and colleagues (Halpern et al., 2004; Halpern & Zatorre, 1999; Zatorre et al., 1996) suggest motor areas are activated in auditory imagery of instrumental (non-vocal) stimuli (Halpern & Zatorre, 1999), and this is consistent with Baddeley and Logie's (1992) claim that the articulatory mechanism is involved in rehearsal of non-vocal stimuli. Relatedly, activation of cerebellar regions involved in control of the tongue and lips occurs during musical imagery (Herholz et al., 2012). Evidence of subvocalization in musical imagery is found in studies of notational audiation, as recognition of a familiar melody embedded within a larger musical score is disrupted more by phonatory interference than by rhythmic or auditory interference (e.g., Brodsky, Henik, Rubenstein, & Zorman, 2003), and EMG 🖟 activity near the larynx is increased during reading of a musical score (Brodsky, Kessler, Rubenstein, Ginsborg, & Henik, 2008).

Mental Practice and Performance

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The distinction between the inner ear and inner voice suggests motor information contributes to auditory imagery, and a role for motor information in auditory imagery can be seen in studies of the effects of musical imagery in mental practice and performance. The role of mental imagery in musical performance is reviewed in detail in Keller (2012), and findings most relevant to understanding neural mechanisms of musical imagery are briefly considered here. When string players performed or imaged a performance of a specific piece, the times taken to play or image were highly correlated, and frontal lobes, cerebellum, parietal lobe, and supplementary motor area, but not primary auditory cortex, were activated during imagery (Langheim, Callicott, Mattay, Duyn, & Weinberger, 2002). When professional or amateur violinists performed or imaged a performance, somatosensory cortex was activated, and activation was more focused in professionals in imagery and in performance (Lotze, Scheler, Tan, Braun, & Birbaumer, 2003), and it was speculated that musical training strengthened connections between auditory and movement areas of the cortex. Violinists exhibited activation of bilateral frontal opercular regions in preparation for and during musical imagery of performance and during performance (Kristeva, Chakarov, Schulte-Mönting, & Spreer, 2003) and exhibited activation in bilateral frontal opercular regions and in sensorimotor, premotor, and supplementary motor areas during imagery of performance and during performance (Nirkko, Baader, Loevblad, Milani, & Wiesendanger, 2000). Coherence of EEG recorded from near the supplementary motor area of a violoncellist was highest while imagining playing scales, less when imagining playing a familiar piece by Bach, and lowest when listening to the same piece by Bach (Petsche, von Stein, & Filz, 1996).

Pianists who were presented with a musical score and imaged playing it or played it on a silent keyboard exhibited overlap in activation of premotor areas in imagery and in performance, and activation was greater during performance; however, primary motor cortex and posterior parietal cortex were active during performance and not during imagery (Meister et al., 2004). Pianists and non-musicians passively listened to a short piano melody or arbitrarily pressed keys on a soundless keyboard, and in both tasks pianists exhibited increased activation in dorsolateral and inferior frontal cortex, superior temporal gyrus, supramarginal gyrus, and supplementary motor and premotor areas (Bangert et al., 2006). Analogous similarities are observed with comparison of imagery and perception. Pianists who listened to familiar pieces exhibited activation in motor regions appropriate for which fingers would have produced the notes (Haueisen & Knösche, 2001) and exhibited activation in auditory areas when they watched a silent video of someone fingering piano keys (Haslinger et al., 2005). Similarly, when pictures of hand configurations for playing guitar chords were shown, guitar players exhibited greater activation in inferior parietal and ventral premotor cortex than did musically 4 untrained observers (Vogt et al., 2007). However, even though there is overlap between neural areas activated during imagery and neural areas activated during perception or performance, there are unique elements to each (e.g., see Zhang et al., 2017), and it is not necessarily the case that a common area of activation implies a similar mental representation (for discussion, see Linke & Cusack, 2015).

Experimental participants who scored higher on a test of auditory imagery performed better on a subsequent performance following practice on a silent keyboard in which auditory feedback was not provided (Highben & Palmer, 2004). Guitarists or vocalists who used mental practice and physical practice performed best with a mixture of mental and physical practice (Theiler & Lippmann, 1995), and mental practice was more effective when musical pieces were relatively easy and less effective than physical practice when musical pieces were more difficult (Cahn, 2008). Pitch encoding of piano students is enhanced if those students make finger tapping movements as if they were playing a piano (Mikumo, 1994), and pitch acuity in auditory imagery and ability to synchronize in a tapping task are positively correlated (Pecenka & Keller, 2009). Relatedly, imaged tempo of popular music is more accurate when individuals tap as they image (Jakubowksi et al., 2016). Imaged singing activates parietal and motor areas including Broca's area and its right hemisphere homologue (e.g., Baumann et al., 2007) and also activates areas associated

with emotional processing including anterior cingulate cortex, anterior temporal lobe, and bilateral amygdala (Kleber, Birbaumer, Veit, Trevorrow, & Lotze, 2007). A case study of a pianist suggested imagery aided in managing tasks and integration of intention and action (Davidson-Kelly, Schaeffer, Moran, & Overy, 2015). In general, mental practice can facilitate subsequent performance (Driskell, Copper, & Moran, 1994; Lotze, 2013), presumably because musical imagery reinforces or strengthens connections made during physical practice, and this suggests a role of motor activation and motor processes in musical imagery.

Dance

Perhaps the most obvious form of embodiment of musical information is dance, which involves production of bodily movements that map onto properties of music. In general, movements of the body can parallel (mimic) movements in music (e.g., slowing near the end of a movement, as when runners slow before stopping and ritardandi occur at the end of a musical piece, e.g., Friberg & Sundberg 1999), and movements of the body in response to a specific piece of music can reflect the rhythm, tempo, meter, and articulation of that music (Fraisse, 1982; Mitchell & Gallaher, 2001). Whether musical imagery influences kinesthetic information in dance, and whether kinesthetic information in dance influences musical imagery, is not known. Given that auditory imagery preserves structural and temporal information of the referent stimulus (Hubbard, 2010, 2013a, 2013b), coupled with structural similarity of music and dance (Krumhansl & Schenck 1997; Vines, Krumhansl, Wanderley, & Levitin, 2006), relationships between kinesthetic imagery of dance and auditory imagery of music (which would contain kinesthetic 🖟 information) could be predicted. Such relationships might influence behavior (e.g., musical imagery of ascending or high pitches might facilitate rising or sustained bodily movement, musical imagery of legato musical notes might facilitate smoother bodily movement, etc.) as well as produce similar patterns of cortical activation. Relatedly, findings that auditory stimuli facilitate non-dance body movements (e.g., in Parkinson's disease; Rizzonelli, Kim, Gladow, & Mainka, 2017; Sabaté et al., 2008; Thaut et al., 1996) suggest auditory imagery of music might be useful in the treatment of motor disorders.

Musical Affect

The evolutionary origins of music have been linked to communication of emotional information (e.g., Bryant, 2013; Snowdon, Zimmerman, & Altenmüller, 2015), and this might account for the common observation of a link between music and affect (for review, see Juslin & Sloboda, 2001). Indeed, music perception increases activation in mesocorticolimbic areas, especially in the amygdala and hippocampus (e.g., Blood & Zatorre, 2001; for review, Koelsch, 2010). Listening to music is linked with release of dopamine in dorsal and ventral striatum, and the amount of dopamine released appears related to the amount of pleasure experienced (Salimpoor, Benovoy, Larcher, Dagher, & Zatorre, 2011). Furthermore, perception of music is linked with an increase of oxytocin (Chanda & Levitin, 2013), which is linked with social bonding. To the extent that musical imagery involves activation of the same neural mechanisms as music perception, cognition, and production, then musical imagery would presumably be linked with affect. Indeed, as noted earlier, the majority of cases of earworms are generally pleasant. Also, if images function as anticipatory predictive processes (e.g., Neisser, 1976; Tian & Poepple, 2012), then matching of musical imagery to subsequent music perception might result in positive affect resulting from a successful prediction (cf. expectancy as a contributor to emotion; Huron, 2006; Juslin & Västfjäll, 2008). Given that perceived music might activate different cortical areas as a function of whether that music is perceived as happy or sad (Khalfa et al., 2005; Mitterschiffthaler, Fu, Dalton, Andrew, & Williams, 2007), analogous patterns of cortical activation could be predicted during music imagery.

Summary and Conclusions

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Musical imagery is phenomenologically similar to music perception, cognition, and production, and studies of musical imagery are often modeled on studies of music perception, cognition, and production. Studies of musical imagery have included behavioral and psychophysical measures, clinical studies of brain-damaged patients, and electroencephalography and brain imaging measures. These studies often found or suggested parallels between neural mechanisms involved in music perception, cognition, and production and neural mechanisms involved in musical imagery. Musical imagery leads to 4 emitted potentials similar to evoked potentials in music perception, and mismatches between perception and imagery can influence ERP components such as N1, N2, P2, LPC, and MMN. Auditory association areas in frontal and prefrontal cortex are activated during musical imagery, and the right temporal lobe seems critical for generation and judgment of pitch. Greater vividness of musical imagery is linked with greater activation in right superior temporal gyrus and prefrontal cortex, and manipulation of musical imagery activates intraparietal and frontal regions activated in other spatial tasks. However, there are some differences in activation patterns; for example, primary auditory cortex is usually activated in music perception but is usually not activated in music imagery. Overall, neural mechanisms involved in musical imagery, like neural mechanisms involved in music perception, cognition, and production, are distributed throughout the cerebral hemispheres and the cerebellum.

An initially surprising finding was that motor areas of the cortex are often activated during musical imagery. This suggests that motor information might contribute to musical imagery, and in fact, motor information has been suggested to contribute to auditory imagery more generally. Researchers proposed a distinction between the inner ear, which involves auditory information, and the inner voice, which involves articulatory information in addition to auditory information. Studies in which the possibility of subvocalization was manipulated support such a distinction. Relatedly, studies of imagery in musical practice and performance highlight how motor activation and information contribute to musical imagery and how musical imagery contributes to performance. Similarly, engagement of the motor system (e.g., tapping along with the beat) improves accuracy of musical imagery, and there is greater activity in motor areas for musicians observing a musical performance on their trained instrument than for non-musicians observing the same performance. The role of the motor system in musical imagery is consistent with an embodied cognition approach and with spatial and force metaphors in the representation of music. Relatedly, mimicry in the form of covert (e.g., neural activation) or overt action is involved in music perception and musical imagery, and music perception and musical imagery might influence our motor system (e.g., dance). Indeed, given the connection between motor activation in music and effects of music on brain plasticity, it could be predicted that musical imagery might be a useful adjunct in treatment of some motor disorders.

Musical imagery occurs in a wide range of domains. Imagery can be voluntary, and it is these voluntary images that previously received the most study. Musical imagery can also occur involuntarily, and examples of involuntary musical imagery include anticipatory musical imagery, pathologies such as musical hallucinations and schizophrenia, and earworms. Anticipatory musical imagery predicts upcoming musical experience, and this is similar to the predictive aspects of other types of imagery and might contribute to musical affect. Relatedly, affective reactions to perceived music are linked to specific neurochemicals and areas of cortical activation, and it could be predicted that musical imagery might involve those same mechanisms. Earworms reflect the common experience of a melodic fragment that individuals "cannot get out of their heads," and although there have recently been many studies focusing on descriptive phenomenology and 4 behavioral correlates of earworms, there have been few studies examining neural mechanisms of earworms. It can be predicted that neural mechanisms of involuntary imagery will presumably overlap with the neural mechanisms involved in voluntary imagery, and any observed

differences in activation patterns could inform not just theories of musical representation, but theories of cognitive control more generally. Overall, musical imagery occurs in a variety of situations; involves neural mechanisms involved in music perception, cognition, and production; is an important part of subjective experience; and reflects the embodied nature of cognition.

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Notes

Interestingly, a number of prominent composers are suspected of or have admitted to experiencing synesthesia in which musical stimuli evoked different colors or other visual qualities (e.g., Leonard Bernstein, Duke Ellington, Billy Joel, Franz Liszt, Oliver Messiaen, Nikolai Rimsky-Korsakov, Alexander Scriabin). The greater prevalence of non-musical imagery (e.g., visual color) triggered by a musical stimulus (e.g., pitch), coupled with the relative lack of musical imagery (e.g., pitch) triggered by a non-musical stimulus (e.g., visual color), is consistent with findings that auditory stimuli evoke non-auditory qualities in a large percentage of synesthetes, but non-auditory stimuli evoke auditory qualities in a very small percentage of synesthetes (Spiller, Jonas, Simner, & Jansari, 2015). Also, it is not clear if the apparent lack of auditory imagery induced in synesthesia is due to a limitation of synesthesia or to a bias in reporting.