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Expert athletes activate somatosensory and motor planning regions of the brain when passively listening to familiar sports sounds

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ABSTRACT

The present functional magnetic resonance imaging study examined the neural response to familiar and unfamiliar, sport and non-sport environmental sounds in expert and novice athletes. Results revealed differential neural responses dependent on sports expertise. Experts had greater neural activation than novices in focal sensorimotor areas such as the supplementary motor area, and pre- and postcentral gyri. Novices showed greater activation than experts in widespread areas involved in perception (i.e. supramarginal, middle occipital, and calcarine gyri; precuneus; inferior and superior parietal lobules), and motor planning and processing (i.e. inferior frontal, middle frontal, and middle temporal gyri). These between-group neural differences also appeared as an expertise effect within specific conditions. Experts showed greater activation than novices during the sport familiar condition in regions responsible for auditory and motor planning, including the inferior frontal gyrus and the parietal operculum. Novices only showed greater activation than experts in the supramarginal gyrus and pons during the non-sport unfamiliar condition, and in the middle frontal gyrus during the sport unfamiliar condition. These results are consistent with the view that expert athletes are attuned to only the most familiar, highly relevant sounds and tune out unfamiliar, irrelevant sounds. Furthermore, these findings that athletes show activation in areas known to be involved in action planning when passively listening to sounds suggests that auditory perception of action can lead to the re-instantiation of neural areas involved in producing these actions, especially if someone has expertise performing the actions.

1. Introduction

When thinking of top athletes in the world, Michael Jordan and Serena Williams quickly come to mind as prototypes for basketball and tennis respectively. But what sets these expert athletes above other athletes who never make it to the professional level? Basketball and tennis are both fast-paced, interactive sports that require an athlete to perform a number of perceptual, cognitive, and motor skills in very brief periods of time. In order to succeed in these sports, an athlete must locate and identify the relevant perceptual cues, make a decision about what these cues mean, and plan and execute the appropriate motor response accordingly. Oftentimes all of this happens so quickly that movements must be initiated with very limited perceptual information. Research has shown that this ability to quickly and accurately process domain-specific information is one of the defining features of expertise; experts are consistently faster and more accurate than novices on a number of perceptual–cognitive paradigms (Hodges, Starkes, & MacMahon, 2006; Mann, Williams, Ward, & Janelle, 2007; Starkes & Ericsson, 2003). Furthermore, this expert advantage in sport may be associated with increased activity in sensory and motor regions of the brain during visual processing tasks (Beilock, Lyons, Mattarella-Micke, Nusbaum, & Small, 2008; Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005; Calvo-Merino, Grezes, Glaser, Passingham, & Haggard, 2006). However, despite widespread global participation in sports and its influence on society, there have been relatively few neuroimaging studies to analyze the expert advantage in sport, especially in the auditory domain.

1.1. Behavioral evidence of an expert advantage in sport

There is considerable behavioral evidence for an expert advantage in sport. This advantage has been observed across numerous sports and a variety of perceptual–cognitive paradigms. Experts tend to perform better than novices on sport-specific attention allocation, object recognition and recall, temporal and spatial occlusion, visual search, anticipation, and decision-making

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(Abernethy, 1990, 1991; Abernethy, Gill, Parks, & Packer, 2001; Abernethy, Neal, & Koning, 1994; Abernethy & Russell, 1987; Abernethy, Zawi, & Jackson, 2008; Hodges et al., 2006; Jackson, Warren, & Abernethy, 2006; Starkes & Ericsson, 2003; Voss, Kramer, Basak, Prakash, & Roberts, 2010; Williams & Ford, 2008; Williams, Ward, & Smeeton, 2004; Wright, Bishop, Jackson, & Abernethy, 2010). A concrete example of this expert advantage in sport is that tennis experts are able to use early visual cues to anticipate the manner and direction in which the ball will come off the racquet, whereas novices are not (Goulet, Bard, & Fleury, 1989; Overney, Blanke, & Herzog, 2008; Shim, Carlton, Chow, & Chae, 2005; Williams, Ford, Eccles, & Ward, 2011). Although action execution is obviously necessary as well, these perceptual and cognitive skills are at least as important, if not more, for successful athletic performance (Ward, Williams, & Bennett, 2002).

1.2. Neural correlates of auditory and action perception

Given that the mastery of a sport typically involves perceptual and cognitive processing of auditory and visuo-motor cues, it is important to note the patterns of neural activation that sub-serve these processes. Several neuroimaging studies have found that environmental sound recognition activates bilateral brain regions including the IFG,[1] MTG,[2] STG[3] (Binder et al., 2000; Demonet et al., 1992; Dick et al., 2007; Lewis, Brefczynski, Phinney, Janik, & DeYoe, 2005; Lewis et al., 2004; Wright et al., 2010), SMG,[4] and posterior cingulate gyrus (Lewis et al., 2004).

IFG has been implicated in motor planning across a number of domains (Hillis et al., 2004; Iseki, Hanakawa, Shinozaki, Nankaku, & Fukuyama, 2008; Liakakis, Nickel, & Seitz, 2011; Ozdemir, Norton, & Schlaug, 2006; Parks et al., 2011; Tettamanti et al., 2005; Wadsworth & Kana, 2011) and may be involved when listening to action-related sounds (Lahav, Saltzman, & Schlaug, 2007), whereas posterior MTG has previously been associated with the recognition of tools and with high-level visual processing of complex biological motion (Beauchamp, Lee, Haxby, & Martin, 2003; Safford, Hussey, Parasuraman, & Thompson, 2011). In addition, it has been suggested that posterior MTG may be particularly important for processing multimodal information and may embody some type of action knowledge that is recruited for the recognition of familiar environmental sounds (Leech & Saygin, 2011; Murray, Camen, Spierer, & Clarke, 2008). Similarly, the left SMG may play a role in audio-tactile associations that emerge for sounds that are often manipulated by the right hand (Lewis et al., 2004). Embodied theories of cognition have explained a similar phenomenon in linguistic processing by proposing that perceptual and motor regions work together with language areas to enable comprehension and production of complex, meaningful sounds. It may be that environmental sounds have similar sensorimotor demands. In fact, studies have found neural activation specific to action-related sounds in left premotor areas (Galati et al., 2008; Pizzamiglio et al., 2005) as well as temporal areas, including MTG (Galati et al., 2008) and posterior STG (Pizzamiglio et al., 2005). Although STG has been shown to be activated when processing environmental sounds, this region may not be activated as selectively as MTG, and may have more to do with lower-level aspects of sound recognition (Lewis et al., 2005). PCC[5] activation during environmental sound processing may be involved in retrieving information from long term memory to determine if the sound is familiar or not (Lewis et al., 2004). Since several studies have demonstrated that participants exhibit a preference or advantage for familiar sounds compared to unfamiliar sounds (Jacobsen, Schroger, Winkler, & Horvath, 2005), the aforementioned neural regions (IFG, MTG, STG, SMG, PCC) may show differential neural activation for familiar and unfamiliar sounds.

1.3. Neural correlates of expertise

There is strong evidence that training and skill acquisition may cause changes in neural activation, especially in the case of expert skill performance (Hill & Schneider, 2006; Wright, Bishop, Jackson, & Abernethy, 2011). These neural changes as a result of training are particularly clear for primary motor areas in the brain. For instance, expert musicians have enlarged representations of their fingers in the primary motor cortex (Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995). There is also evidence that this expertise effect may carry over into the perception of action. Calvo-Merino et al. (2005) found motor expertise effects in bilateral premotor cortex and intraparietal sulcus, right superior parietal lobe, and left posterior superior temporal sulcus for two different types of dancers (ballet and capoeira martial artists) when passively viewing an action being performed by someone else. Interestingly, the neural response differed depending on the viewers' own expertise with executing the specific action; expert dancers had stronger BOLD[6] activation in motor areas of the brain when they observed actions from their own type of dance than when they observed kinematically similar actions in the other type of dance. Similarly, when ballet dancers viewed gender-specific dance moves, greater activation was observed in premotor, parietal, and cerebellar regions when viewing moves with which the observer had personal experience (Calvo-Merino et al., 2006). In short, these studies reveal that there may be expertise effects in action perception, and that these effects may appear as an increased neural response in motor regions of the brain.

Beilock et al. (2008) also found motor expertise effects in a fMRI experiment with three varying levels of hockey expertise: player, fan, and novice. Results revealed a positive correlation between hockey experience and neural activity in left dorsal premotor cortex, a region usually implemented in higher-level action selection and implementation (Haslinger et al., 2002), and a negative correlation between hockey experience and activity in right sensory-motor cortex, a lower level sensory-motor region implicated in the instantiation of movement (Bedard & Sanes, 2009; Mancini et al., 2009). Taken together these results suggest that experts engage in motor preparation in response to the perception of highly familiar stimuli, and that this has to do with their expertise with executing the specific action (Beilock et al., 2008; Calvo-Merino et al., 2005, 2006). However, the majority of these studies focused on athletic expertise in the visual modality. Auditory expertise has not been examined in the domain of sport, but an effect is likely, especially given that auditory expertise effects have been observed in musicians, specifically in premotor regions of the brain (Dick, Lee, Nusbaum, & Price, 2011; Margulis, Mlsna, Uppunda, Parrish, & Wong, 2009; Ohnishi et al., 2001). Given the high relevance of auditory perceptual cues to successful athletic performance, athletic expertise in the auditory domain merits further investigation (Chartrand, Peretz, & Belin, 2008).

1.4. Present study

The purpose of the present fMRI study was to examine whether athletic expertise influenced the neural correlates of passive sound perception. To accomplish this, a 2 (expertise) $\times$ 4 (sound type) experimental design was employed. Participants were either

[1] Inferior frontal gyrus.
[2] Middle temporal gyrus.
[3] Superior temporal gyrus.
[4] Supramarginal gyrus.
[5] Posterior cingulate cortex.
[6] Blood–oxygen level dependent.

expert or novice athletes, and sounds were familiar and unfamiliar, sport and non-sport sounds. This yielded four conditions of sound types: SF,[7] SU,[8] NF,[9] and NU.[10] The stimuli for the SF and SU condition were tailored to each individual based on which sport they played; thus, sport sounds were initially coded as sport basketball and sport tennis, then aligned to the appropriate SF and SU condition for each participant. For example, for a tennis player, the tennis sounds were considered the SF condition, and the basketball sounds were considered the SU condition, whereas for a basketball player, the basketball sounds were the SF and the tennis sounds were the SU. The NF and NU conditions were constant across participants.

Consistent with previous research on environmental sound processing and action perception, the present passive listening fMRI task with athletes was expected to elicit activity in IFG, MTG, STG, and premotor cortex (Beilock et al., 2008; Binder et al., 2000; Buccino et al., 2004; Calvo-Merino et al., 2005; Demonet et al., 1992; Dick et al., 2007, 2011; Galati et al., 2008; Lewis et al., 2004, 2005; Pizzamiglio et al., 2005; Wright & Jackson, 2007). The extent of activation in these areas was of particular interest for the sport familiar condition, in which expertise differences were greatest. Increased activity across frontal, temporal and premotor cortex in the sport familiar condition would suggest that expertise leads to recruitment of these areas when no explicit task is required. Finally, it was of interest to compare experts and novices in processing sport unfamiliar and environmental sounds. Given the literature reviewed earlier, it is likely that experts who are trained to ignore irrelevant sounds may show less neural activation for environmental stimuli relative to novices.

2. Method

2.1. Participants

Participants were fifty-seven right-handed athletes who actively played basketball or tennis at the college varsity (expert) or recreational (novice) level and lived in the Houston metropolitan area. Participants had only ever played basketball or tennis, but never both. An additional eight participants ($N_{\text{experts}} = 2$, $N_{novices} = 6$) were excluded from the fMRI portion of the experiment due to regular experience with the other sport (basketball or tennis), in addition to their primary sport, at some point in their life. Experts ($N_{\text{experts}} = 27$; 18 females; $M_{\text{age}} = 20.81$; $M_{\text{AoA}} = 8.30$, $M_{\text{years}} = 12.67$, $M_{\text{practice}} = 14.44$) and novices ($N_{novices} = 30$; 11 females; $M_{\text{age}} = 21.70$; $M_{\text{AoA}} = 10.17$, $M_{\text{years}} = 11.43$, $M_{\text{practice}} = 4.92$) did not differ on current age (F (1, 55) = 1.10, p = n.s.) or number of years played (F (1, 55) = 1.13, p = n.s), but did differ on AoA[11] (F (1, 55) = 4.46, $p = .039$) and average number of hours practiced per week (F (1, 55) = 146.23, $p < .0001$). See Table 1 for a summary of demographic and behavioral data.

2.2. Materials

The experimental stimuli, listed in Appendix A, consisted of a set of 20 environmental sounds derived from artificial, manipulable objects. Ten were sport sounds ($N_{\text{tennis}} = 5$, $N_{\text{basketball}} = 5$) prepared by researchers of the present study, and ten were non-sport sounds ($N_{\text{familiar}} = 5$, $N_{\text{unfamiliar}} = 5$) from Marcell, Borella, Greene, Kerr, and Rogers's (2000) normative sound archives. Each stimulus was approximately 1220 ms, and was presented four times, in randomized order, during the fMRI experiment for a total of 80 trials, 20 per condition. Non-sport sounds were composed of common environmental sounds such as a toilet flushing or paper crumpling. Sport sounds were composed of sounds from tennis and basketball, including five variations of a basketball bouncing on a court, and five variations of a tennis ball being hit by a racquet. The sport sounds varied slightly in terms of how many times and how hard the ball was bounced or hit. All 20 sounds were tested behaviorally in an unpublished normative study conducted in our laboratory, during which 29 novice athletes who did not participate in the fMRI study were asked to identify each sound. All 20 sounds were correctly identified by at least 90% of the participants. It is important to note that the familiarity classification is based on the identifiability of the sound, as opposed to the commonality of the sound. For instance, someone may frequently hear paper being crumpled into a ball, but the "paper crumbling" sound is still generally unfamiliar and difficult to identify. Likewise, the sport sounds from the unfamiliar sport may have been heard by the participant at some point in his/her life, but are still generally unfamiliar and more difficult to identify. Thus, the familiarity classification is relative rather than absolute, and as such, familiarity was not treated as a separate factor in the fMRI analyses.

2.3. Measures

Participants completed a consent form as well as a series of prescreening forms relevant for the fMRI portion of the experiment, including a claustrophobia screening form, metal screening form, and handedness screening form. They were also asked to complete two questionnaires developed in our labs, the Athletic Background Questionnaire (Appendix B) and Collegiate Athlete Questionnaire (Appendix C), to gain information regarding their athletic background such as which sports they played, AoA of each sport, how many years they played each sport and at what level, and how many hours a week they currently practiced each sport.

2.4. Procedure

Informed consent was obtained from participants in accordance with Institutional Review Boards at Baylor College of Medicine and the University of Houston. After giving consent and completing the necessary prescreening forms and questionnaires, participants were scheduled for their fMRI session at the Human Neuroimaging Laboratory at Baylor College of Medicine in Houston Texas. During the fMRI experiment, a computer running Networked Experiment Management Objects (NEMO; Houston, TX) presented a series of sounds to the participants binaurally through fMRI-compatible headphones. The experimental stimuli consisted of 10 sport sounds ($N_{\text{tennis}} = 5$, $N_{\text{basketball}} = 5$) and 10 non-sport sounds ($N_{\text{familiar}} = 5$, $N_{\text{unfamiliar}} = 5$), all of which were presented four times in a randomized order for a total of 80 test trials. These test trials were separated by four baseline trials during which no auditory stimuli were presented. The functional portion of the experiment lasted approximately 24 min. Upon completion of the study, participants were compensated with $45.

As demonstrated in Fig. 1, CVA[12] was used so that scanner noise did not interfere with presentation of the auditory stimuli. Each stimulus was presented between image acquisitions during the middle of a 1560 ms period of scanner silence. Participants were instructed to listen to the sounds and told they might be asked about them later to encourage them to attend to the sounds, but were never actually asked about the sounds. Possible motor activation was expected as a result of the task itself, so an overt behavioral response was avoided in order to eliminate confounding motor activity resulting from a button response with that associated with a particular auditory stimulus.

[7] Sport familiar.
[8] Sport unfamiliar.
[9] Non-sport familiar.
[10] Non-sport unfamiliar.
[11] Age of acquisition.
[12] Clustered volume activation.

Table 1
Demographic and behavioral data.

		Experts	Novices	F (1, 55)	ANOVA	Overall total/mean
Demographic information	*n*	26	31			57
	Age	20.81 (3.3)	21.70 (3.1)	1.10	p = n.s.	21.28 (3.2)
Athletic background	AoA	8.30 (3.3)	10.17 (3.4)	4.46	$p = .039^*$	9.28 (3.4)
	Years played	12.67 (4.1)	11.43 (4.6)	1.13	p = n.s.	12.02 (4.4)
	Practice (hrs/wk)	14.44 (2.4)	4.92 (3.4)	146.23	$p < .0001^*$	9.43 (5.6)

* $p < .05$

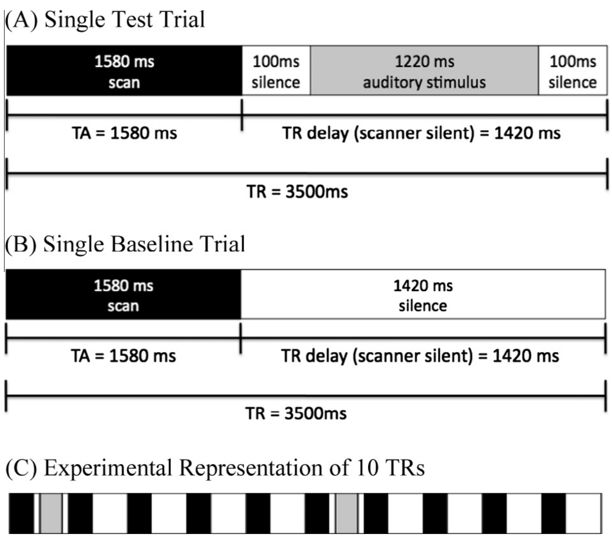

Fig. 1. Experimental design, clusteredvolumeactivation. (A) Single testtrial. On test trials, participants heard a 1220 ms auditory stimulus presented in the middle of the 1420 ms silent period between scans. (B) Single baselinetrial. On baseline trials, participants did not hear anything during the 1420 ms silent period between scans. (C) Experimental representation of 10 TRs. In order to allow for the hemodynamic response to return to baseline, each test trial was followed by 4 baseline trials before repeating another test trial.

2.5. Imaging parameters

A 3.0 T Magnetom Trio (Siemens, Germany) scanner in the Human Neuroimaging Lab at Baylor College of Medicine was used for the fMRI session. Structural images were obtained during a four and a half minute T_1-weighted MP-RAGE[13] sequence optimized for grey-white matter contrast. During this time, 192 whole brain saggital scans were acquired with a slice thickness of 0.89 mm and an in-plane resolution of 0.96 mm × 0.96 mm. Functional images were acquired using T_2^*-weighted gradient-echo EPI[14] sequence sensitive to BOLD signal. A CVA paradigm was used to acquire 33 transverse slices in a descending order with 30 ms TE,[15] 3500 ms TR,[16] 1560 ms TR delay, 1940 ms TA,[17] 90-degree flip angle, 4 mm slice thickness, and 3.44 mm × 3.44 mm in-plane resolution.

2.6. Imaging analyses

Preprocessing and statistical analyses of the fMRI images were performed using Statistical Parametric Mapping 8 (SPM8; Friston, 1995) running on Matlab7.8 (The Mathworks, Natwick, Massachusetts). Prior to analysis, functional images were corrected for slice timing artifacts, realigned to the anatomical scans, co-registered with a canonical brain in MNI coordinates, segmented, normalized (reslicing the voxels to 2 × 2 × 2 mm^3), and smoothed with an 8 mm FWHM[18] isotropic Gaussian kernel in order to increase signal-to-noise ratio. The first four volumes acquired for each participant were removed from analyses so as to allow for stabilization of the BOLD signal.

Statistical analyses were also performed using SPM8 (Wellcome Department of Cognitive Neurology, Institute of Neurology, London, UK) and consisted of two levels of analyses. The first level involved a fixed effect analysis to create t-contrast images for each participant for the four experimental conditions: SF, SU, NF, and NU. These were then entered into a second level random effects analysis to determine cortical regions that were activated within- and between-group. A 2 (Group: Expert, Novice) × 4 (Sound Type: SF, SU, NF, NU) ANOVA was entered as a full factorial analysis in SPM8, with direct contrasts performed as independent samples *t*-tests. All resulting images were corrected for intensity using a threshold value of $p < .001$ uncorrected and extent threshold minimum of 20 voxels. Figures were displayed using xjView toolbox (http://www.alivelearn.net/xjview).

3. Results

3.1. Behavioral results

A MANOVA was conducted with expertise (expert and novice) as a between-subject factor, and age, AoA, years played, and amount of practice as within-subject factors, with a significance threshold of $p < .05$. This analysis indicated that experts and novices were significantly different in terms of AoA, F (1, 55) = 4.45, $p = .039$ ($M_{expert} = 8.30$, $SD = 3.3$; $M_{\text{novice}} = 10.17$, $SD = 3.4$), and number of hours practiced per week, F (1, 55) = 146.23, $p < .0001$ ($M_{expert} = 14.44$, $SD = 2.4$; $M_{\text{novice}} = 4.92$, $SD = 2.4$). However, athletes did not differ on current age, F (1, 55) = 1.10, p = n.s. ($M_{expert} = 20.81$, $SD = 3.3$; $M_{\text{novice}} = 21.70$, $SD = 3.1$), or number of years played, F (1, 55) = 1.13, p = .292 ($M_{expert} = 12.67$, $SD = 4.1$; $M_{\text{novice}} = 11.43$, $SD = 4.6$). See Table 1. This suggests that any group differences between experts and novices were likely due to cumulative amount of experience with their sport.

3.2. Neuroimaging results

A 2 (Group: Expert, Novice) × 4 (Sound Type: SF, SU, NF, NU) ANOVA revealed a main effect of group and main effect of sound type, but no interaction of group by sound type. As expected, between-group analyses revealed significant differences in neural activation between expert and novice athletes. Expert athletes had greater neural activity than novice athletes in a number of brain areas including bilateral STG, right precentral gyrus, and left cingulate gyrus. The reverse comparison of novices greater than experts showed more widespread activation in frontal, temporal,

[13] Magnetization-prepared radio-frequency pulse and rapid gradient-echo.
[14] Echo-planar-imaging.
[15] Echo time.
[16] Repetition time.
[17] Acquisition time.
[18] Full-width half-maximum.

Table 2
Clusters of activation for experts and novices, collapsed across condition.

Region	Voxels	Side	x	y	z	Z
Experts > Novices						
Cingulate Gyrus	131	L	−12	12	36	5.02
STG	70	L	−54	−38	14	4.51
STG	32	L	−54	−16	4	4.07
STG	32	R	62	−24	8	3.93
Precentral Gyrus	28	R	36	2	30	3.66
Novices > Experts						
SMG	143	L	−54	−26	14	5.30
Precuneus	171	R	20	−52	20	4.36
MFG	86	R	44	12	46	4.22
IPL	112	L	−32	−40	42	4.14
MTG	66	L	−48	−24	−14	4.10
MOG	61	R	38	−72	34	4.05
SPL	42	L	−10	−60	64	3.92
IFG	84	R	58	22	12	3.86
MTG	45	R	50	−14	−12	3.71
Calcarine gyrus	69	L	−14	−58	12	3.70
SPL	25	R	32	−62	54	3.54

parietal, and occipital areas, including areas involved in perceptual processing (i.e. left SMG, right precuneus, left IPL,[19] bilateral SPL,[20] right MOG,[21] left calcarine gyrus), and motor planning and processing (i.e. right IFG, right MFG,[22] bilateral MTG). These areas are displayed in Table 2 and Fig. 2.

When the expert and novice groups were collapsed together, participants showed differential neural response to sport and non-sport sounds. The resulting areas from the contrasts are displayed in Table 3 and Fig. 3. Consistent with previous research, when passively listening to non-sport environmental sounds athletes recruited large areas of bilateral STG (Dick et al., 2007; Lewis et al., 2004, 2005), as well as bilateral ACC,[23] bilateral thalamus, bilateral cerebellum, and left hippocampus. This suggests that when processing non-sport sounds, athletes utilized a broad, perceptual–cognitive–motor network involving auditory perception, attention, memory, and motor control. More interestingly, when passively listening to sport sounds, athletes recruited more direct motor areas including bilateral SMA,[24] left precentral gyrus, and bilateral postcentral gyri. Additionally, when athletes were collapsed across groups, there was a significant effect of familiarity for sport sounds. All athletes recruited greater activation for the SF condition compared to the SU condition in the right superior frontal region corresponding to BA 6/SMA. There was no significant activation for sport unfamiliar compared to sport familiar sounds (Table 3). These regions are often implicated in motor imagery (Malouin, Richards, Jackson, Dumas, & Doyon, 2003; Porro, Cettolo, Francescato, & Baraldi, 2000; Shergill et al., 2001; Wang, Wai, Weng, Yu, & Wang, 2008), and suggests that athletes may be imagining motor performance in response to sport sounds.

The general between-group neural differences mentioned above also appeared as an expertise effect in specific conditions. Experts showed greater activation than novices only in the SF condition, their area of expertise. This activation appeared to be relatively focal, and in regions typically involved in the observation and imitation of action, such as the IFG and IPC.[25] Novices, on the other hand, showed greater activation than experts only in the NU and SU conditions, recruiting a broader neural network throughout the brain including left SMG, right pons and right MFG. These areas are displayed in Table 4 and Fig. 4. No neural differences were seen between groups in the NF condition, or in experts greater than novices in the NU or SU conditions. These results suggest that expert athletes' brains are attuned to only the most familiar, highly relevant sounds and tune out unfamiliar, irrelevant sounds; novices on the other hand seemingly attended to and processed all sounds, including the unfamiliar ones, in an attempt to make sense of them.

4. Discussion

The present fMRI study examined whether athletic expertise influenced the neural correlates of passive sound perception. In line with our hypotheses, significant differences were found between expert and novice athletes for both sport and non-sport sounds.

4.1. Athletes recruit motor areas of the brain when passively listening to sport sounds

The fascinating part of our results was that when passively listening to sport sounds, athletes recruited motor planning, primary motor, and sensorimotor areas of the brain, including bilateral SMA, left precentral gyrus, and bilateral postcentral gyrus. Although these findings should be interpreted cautiously due to potential differences in the sport and non-sport sounds in terms of diversity and basic acoustical properties, and the uncertainty as to which features of the sounds may be driving the differential activation (Lewis et al., 2005), the current findings are supported by and extend previous research that reports motor activation during auditory perception in other, non-sport domains (Dick et al., 2011; Galati et al., 2008; Lahav et al., 2007; Lewis et al., 2005; Pizzamiglio et al., 2005). Specifically, SMA is thought to be involved in motor planning, especially for complex motor sequences (Hayes, Elliott, Andrew, Roberts, & Bennett, 2012; Marchand et al., 2013) and may have a direct role in basic motor control especially for coordinating movements involving inter-manual or bimanual coordination (Nair, Purcott, Fuchs, Steinberg, & Kelso, 2003). Pre- and postcentral gyri have been classically associated with motor and somatosensory processing. These motor areas were recruited despite the fact that participants were only instructed to listen to the sounds and were not explicitly asked to generate a response. These areas have also typically been implicated in tasks that elicit motor imagery (Malouin et al., 2003; Porro et al., 2000; Shergill et al., 2001; Wang et al., 2008), and suggests that athletes may be engaged in motor imagery even when passively listening to sport sounds.

4.2. Expert advantage in motor planning for familiar sport sounds

Most notably, a processing advantage for highly familiar sport sounds was found for expert athletes. Despite the fact that all stimuli were purely auditory and participants were not explicitly asked to generate a response, expert athletes showed increased activity in the IFG and the parietal operculum when listening to sounds from their own sport. The IFG and the parietal operculum have been implicated in the observation and imitation of action (Buccino et al., 2004; Calvo-Merino et al., 2005, 2006; Caspers, Zilles, Laird, & Eickhoff, 2010; Wright & Jackson, 2007). Studies with mirror neurons in macaque monkeys (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996) and humans (Iacoboni et al., 1999) have linked areas in the IFG to action observation. These mirror neurons in IFG may also be involved when humans listen to action-related sounds (Lahav et al., 2007). In addition, activation in IFG has been linked to motor planning across a number of domains (Hillis et al., 2004; Iseki et al., 2008; Ozdemir et al., 2006; Parks et al., 2011; Tettamanti et al., 2005; Wadsworth & Kana, 2011). Right IFG activity similar to that

[19] Inferior parietal lobule.
[20] Superior parietal lobule.
[21] Middle occipital gyrus.
[22] Middle frontal gyrus.
[23] Anterior cingulate cortex.
[24] Supplementary motor area.
[25] Inferior parietal cortex.

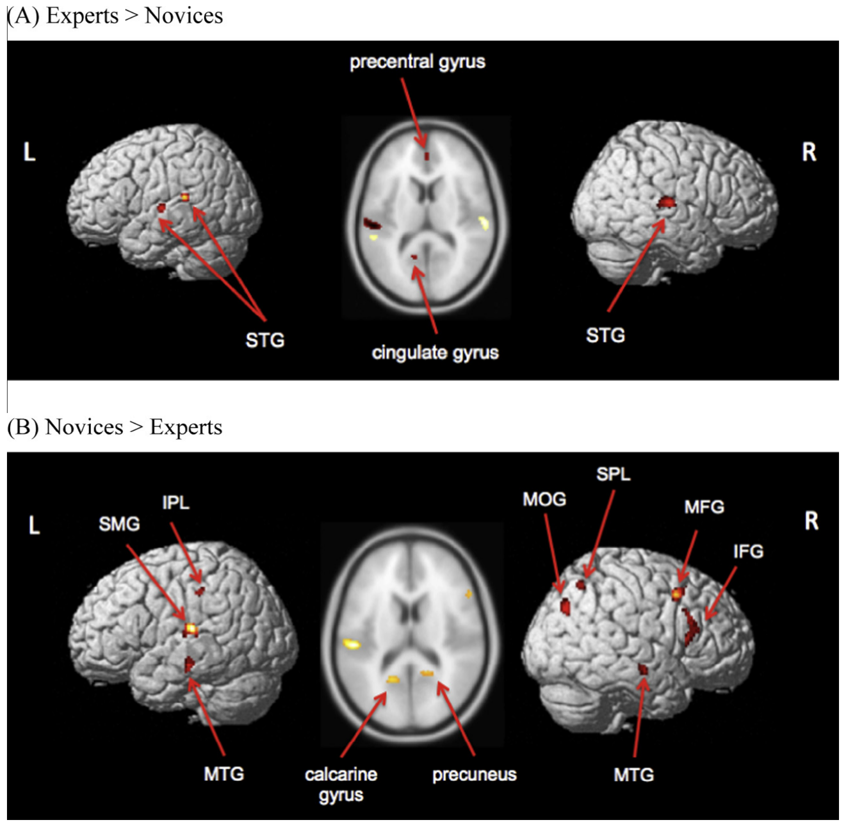

Fig. 2. Between-group clusters of activation for experts and novices collapsed across condition (A) Experts > Novices. (B) Novices > Experts. Images were corrected for intensity using a threshold value of $p < .001$ uncorrected, $k = 20$.

Table 3
Clusters of activation for sport and non-sport conditions, collapsed across expertise.

Region	Voxels	Side	x	y	z	Z
Non-sport > Sport						
STG	2677	R	60	2	−4	6.62
STG	2195	L	−50	−10	2	6.44
ACC	1030	B	2	18	26	4.50
Thalamus	539	B	6	−36	0	4.36
Cerebellum	343	R	32	−72	−32	4.07
Cerebellum	133	L	−22	−74	−28	3.73
Hippocampus	23	L	−16	−24	−10	3.43
Sport > Non-sport						
SMA	106	R	10	−20	64	3.96
Postcentral gyrus	209	L	−54	−22	44	3.94
Postcentral gyrus	184	R	40	−28	50	3.67
Precentral Gyrus	23	L	−28	−16	54	3.38
SMA	24	L	−10	−18	64	3.37
Sport Familiar > Sport Unfamiliar						
SMA	27	R	21	1	67	3.77

observed in the current study has been present when participants are asked to perform an action (Shibata, Inui, & Ogawa, 2011) as well as when asked to attend to an action (Hampshire, Thompson, Duncan, & Owen, 2009). The parietal operculum is proximal to somatosensory cortex and as such is conceptualized as being involved in a person's body sense (Bassetti, Bogousslavsky, & Regli, 1993). This suggests that experts in a sport may link sounds in that sport with a particular motor plan, involving specific body parts, in a more efficient manner than novices. This is the first time to our knowledge that expertise in a sport has been associated with the manner in which auditory processing of sports sounds occur.

4.3. Processing of unfamiliar sounds in novices

The difference in expertise across groups also appeared in the sport unfamiliar condition, but only as increased activity for the novice group. Compared to expert athletes, novices showed greater activation in the right MFG in Broadmann's Area 9. This region has been found to be active during motor processing and imagery (Hanakawa, Dimyan, & Hallett, 2008; Schubotz & von Cramon, 2004). Hence, novice athletes showed more motor activity in their less familiar sport relative to expert athletes. The processing of stimuli outside of the familiar sport for novice athletes was also observed for unfamiliar environmental sounds in the right SMG and the pons. The brainstem is known to show increased activity for auditory stimuli and is conceptualized as being involved in the low-level processing that progresses from the cochlear nuclei up to the auditory cortex (Griffiths, Uppenkamp, Johnsrude, Josephs, & Patterson, 2001; Mehta, Grabowski, Razavi, Eaton, & Bolinger, 2006; Sigalovsky & Melcher, 2006). The SMG, on the other hand, has been found to be involved in the successful retrieval of auditory and visual stimuli when participants fail to form appropriate images for the stimuli (Huijbers, Pennartz, Rubin, & Daselaar, 2011). It has also been suggested that the left SMG may play a role in audio-tactile associations that emerge for sounds that are often manipulated by the right hand (Lewis et al., 2004). Although in this case these were unfamiliar sounds, the athletes may have been using an audio-tactile association strategy to try and identify the object sound based on mental manipulation with their dominant right hand. Hence, it appears that the SMG may be active during identification of these sounds. Taken together, these results suggest that novice athletes process unfamiliar environmental sounds using basic auditory mechanisms and may be attempting to access the objects associated with the sounds.

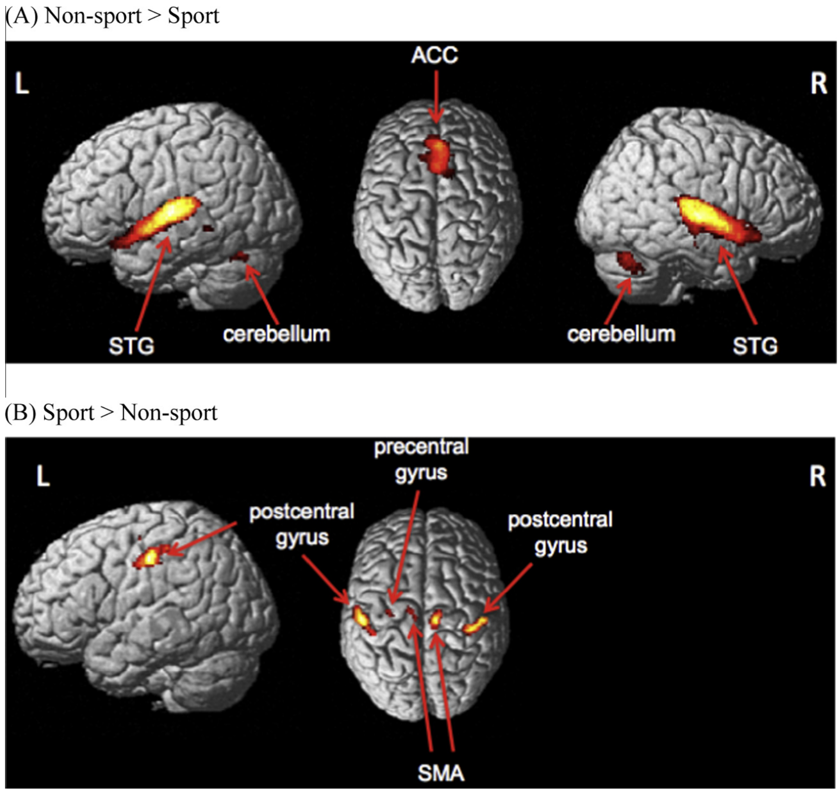

Fig. 3. Clusters of activation for non-sport and sport conditions. (A) Non-sport > Sport condition. (B) Sport > Non-sport condition. Images were corrected for intensity using a threshold value of $p < .001$ uncorrected, $k = 20$.

Table 4
Clusters of activation for experts and novices, within condition.

Region	Voxels	Side	*x*	*y*	*z*	*Z*
SF experts > SF novices						
IPC	24	R	54	−22	26	3.57
IFG	36	R	50	10	20	3.50
SU novices > SU experts						
MFG	56	R	44	14	48	3.52
NU novices > NU experts						
SMG	33	L	−54	−24	16	3.68
Pons	37	R	2	−34	−48	3.52

4.4. Implications

In general, these patterns of results suggest that expert athletes may more readily engage motor planning sequences in response to sounds from their primary sport. Novice athletes, on the other hand, show greater activation for the unfamiliar sport and unfamiliar environmental sounds. This implies that expert athletes may be focusing on the sport sounds in their familiar sport and attending less to the other sounds in their environment. Consequently, novice athletes may be more readily distracted by sounds not related to their most familiar sport. Interestingly, the direct comparisons between expert and novice athletes reveal this dichotomy across the entire set of stimuli regardless of condition. Expert athletes showed focal activity in bilateral sensorimotor areas, including STG, precentral gyrus, and cingulate gyrus. Alternatively, novice athletes showed bilateral activity in frontal, temporal, parietal, and occipital areas more broadly. This included areas involved in perceptual (i.e. SMG, precuneus, IPL, SPL, middle occipital gyrus, calcarine gyrus), and motor planning and processing (i.e. IFG, MFG, MTG). This is consistent with the view that novice athletes were more focused on perceiving and interpreting the auditory stimuli they encountered whereas expert athletes were more focused on preparing a motor response for their primary sport. This was all done without explicit instruction to do so. This leads us to tentatively conclude that expertise in a sport leads to more ready activation of motor sequences associated with a sport and to filtering out of other sounds. The notion that this process is occurring when passively listening to sounds, even when not explicitly asked to imagine anything, suggests that expert athletes may have particularly adept motor imagery skills. Future studies should investigate how this process might change when athletes are explicitly asked to imagine their responses to auditory stimuli.

One interesting caveat is that expertise is a product of the amount of practice, which depends on the time at which an individual began to play a particular sport. Work in our laboratories has found that early learning of a sport may lead to more sensorimotor forms of processing whereas later learning of a sport may lead to more cognitive forms of processing (Hernandez, Mattarella-Micke, Redding, Woods, & Beilock, 2011). The current results are consistent with this view. These results suggest that expertise, which is a product both of when the sport is acquired and how much it has been played across the lifetime, leads to changes in the processing of auditory stimuli under passive conditions. Future studies are needed in order to disentangle how age of initial learning and amount of practice may differentially influence brain activity in expert and novice athletes.

5. Conclusion

The present fMRI study examined whether athletic expertise influenced the neural processing of sounds in expert and novice athletes. Although no behavioral response was required during the task, participants recruited bilateral motor areas including the SMA and pre- and postcentral gyri when listening to sport sounds, suggestive of motor imagery during a passive listening task.

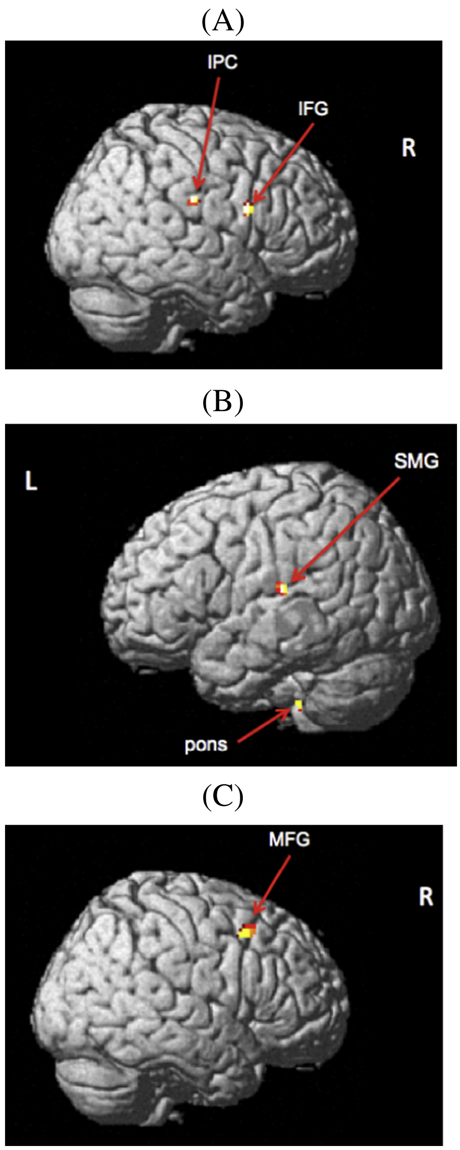

Fig. 4. Between-groupclusters of activation. (A) Sport familiar in Experts > Sport familiar in Novices. (B) Non-sport unfamiliar in Novices > Non-sport unfamiliar in Experts. (C) Sport unfamiliar in Novices > Sport unfamiliar in experts. Images were corrected for intensity using a threshold value of $p < .001$ uncorrected, $k = 20$.

Furthermore, an expert advantage emerged with experts showing greater activation than novices in the IFG and IPC during the familiar sport condition. These findings that experts show activation in brain regions known to be involved in action planning when just passively listening to sounds suggests that auditory perception of action can lead to the re-instantiation of neural areas involved in actually producing these actions, especially if someone has expertise performing the actions. These results may also help to shed light on the reasons that expert athletes are less susceptible to failure in difficult situations; they are simply better at attending to sounds in their sport while ignoring other environmental stimuli.

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Appendix A. Stimuli

	Stimulus	Condition	Sound File Name
1	Camera	NF	NF1.mp3
2	Coin Dropping	NF	NF2.mp3
3	Drums	NF	NF3.mp3
4	Glass Breaking	NF	NF4.mp3
5	Toilet Flushing	NF	NF5.mp3
6	Banjo	NU	NU1.mp3
7	Bike Bell	NU	NU2.mp3
8	Clapping	NU	NU3.mp3
9	Flute	NU	NU4.mp3
10	Paper Crumpling	NU	NU5.mp3
11	Basketball 1	SB	SB1.mp3
12	Basketball 2	SB	SB2.mp3
13	Basketball 3	SB	SB3.mp3
14	Basketball 4	SB	SB4.mp3
15	Basketball 5	SB	SB5.mp3
16	Tennis 1	ST	ST1.mp3
17	Tennis 2	ST	ST2.mp3
18	Tennis 3	ST	ST3.mp3
19	Tennis 4	ST	ST4.mp3
20	Tennis 5	ST	ST5.mp3

Appendix B. Athletic Background Questionnaire

Gender: ________ Age: ________ Today's Date: ____________

Email Address: _______________________

What kind(s) of sporting experience do you have?

Sport	Currently Practice	If Yes, Level*	Start Age	Stop Age	# of Years	Highest Level*	Skill Then**	Skill Now**
____________	Y / N	_____	_____	_____	_____	______	_____	_____
___________	Y / N	_____	_____	_____	_____	______	_____	_____
___________	Y / N	_____	_____	_____	_____	______	_____	_____
___________	Y / N	_____	_____	_____	_____	______	_____	_____
___________	Y / N	_____	_____	_____	_____	______	_____	_____
___________	Y / N	_____	_____	_____	_____	______	_____	_____

*** Please list the # of years at this level, followed by the type of level:**
NCAA = college, C = Club, IM = intramural, HS = high school, MS = middle school, R = recreational/city league
**** Rate your technical proficiency in the sport, then (at your highest level of play) and now, on a scale of 1 to 5:**

1 2 3 4 5
Poor Average Excellent

If you currently practice a sport, how much do you practice? (check 2 boxes)

Sport	0-1pr/wk	2-3pr/wk	4+pr/wk	0-5hr/wk	5-10hr/wk	10-15hr/wk	15+hr/wk
________	_______	_______	_______	_______	_______	_______	_______
________	_______	_______	_______	_______	_______	_______	_______
________	_______	_______	_______	_______	_______	_______	_______
________	_______	_______	_______	_______	_______	_______	_______
________	_______	_______	_______	_______	_______	_______	_______

Have you ever been an instructor, officiate, or team manager of a sport? Y / N

Sport	Your Age	Duration	Capacity (e.g. college varsity coach)
___________	__________	__________	______________________________
___________	__________	__________	______________________________
___________	__________	__________	______________________________
___________	__________	__________	______________________________
___________	__________	__________	______________________________

Do you ever attend sporting events (of any level) as a spectator? Y / N

Sport	Level	Frequency	Average # of games per year
___________	__________	__________	______________________________
___________	__________	__________	______________________________
___________	__________	__________	______________________________
___________	__________	__________	______________________________
___________	__________	__________	______________________________

Do you ever watch sporting events on T.V.? Y / N

Sport	Level	Frequency	Average # of games per year
___________	__________	__________	______________________________
___________	__________	__________	______________________________
___________	__________	__________	______________________________
___________	__________	__________	______________________________
___________	__________	__________	______________________________

Do you ever play sports video games? Y / N

Sport	Game System	Frequency	# hrs/week	Skill Level**
___________	__________	____________	__________	____________
___________	__________	____________	__________	____________
___________	__________	____________	__________	____________
___________	__________	____________	__________	____________
___________	__________	____________	__________	____________

Please describe any other sporting experience you've had that was not mentioned above:

____
____
____
____

Appendix C. Collegiate Athlete Background

Your primary sport: _________________
Age you began playing this sport: ______

PRE-HIGH SCHOOL EXPERIENCES
years playing sport at this level: _______
Please describe team/league/level: ____
____
What positions did you play? ____
List any honors or awards that you or your team received while you were a player: _____
____
____

HIGH SCHOOL EXPERIENCES
years playing sport at this level: _______
Please describe team/league/level: ____
____
What positions did you play? ____
List any honors or awards that you or your team received while you were a player: _____
____
____

COLLEGE EXPERIENCES
years playing sport at this level: _______
Please describe team/league/level: ____
____
What positions did you play? ____
List any honors or awards that you or your team received while you were a player: _____
____
____

What is your dominant hand/foot for this sport?______________________________

Have you had any prolonged lapses in playing this sport? (i.e. have you stopped playing for a month or more)

Date	**Duration**
____/____/____	__________
____/____/____	__________
____/____/____	__________
____/____/____	__________

Do you have any family members who have participated and excelled in your primary sport or other sports? Y / N

If yes:

Which sport(s)? ____

What is their relationship to you? ______________________________________

What was their highest level of experience? ______________________________

On a scale of 1 to 5, how good do you think you are at this sport compared to other people:
your age that currently play? _____
that play at your level? ______
that play your position at your level? _______

1 = One of the Worst
2 = Below Average
3 = Average
4 = Above Average
5 = One of the Best

Please list below or attach any relevant personal statistics from this sport:

Appendix D. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.bandc.2014.03.007.

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