



Review

The auditory dorsal pathway: Orienting vision

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ABSTRACT

A particularly prominent model of auditory cortical function proposes that a dorsal brain pathway, emanating from the posterior auditory cortex, is primarily concerned with processing the spatial features of sounds. In the present paper, we outline some difficulties with a strict functional interpretation of this pathway, and highlight the recent trend to understand this pathway in terms of one that uses acoustic information to guide motor output towards objects of interest. In this spirit, we consider the possibility that some of the auditory spatial processing activity that has been observed in the dorsal pathway may actually be understood as a form of action processing in which the visual system may be guided to a particular location of interest. In this regard, attentional orientation may be considered a low-level form of action planning. Incorporating an auditory-guided motor aspect to the dorsal pathway not only offers a more holistic account of auditory processing, but also provides a more ecologically valid perspective on auditory processing in dorsal brain regions.

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1. Introduction

The ‘decade of the brain’ brought with it many advances in our understanding of the auditory cortical system. By the early 1990s it had become evident that cells in the auditory cortex were not functionally homogeneous. Single-cell research in non-

human primates established that the primary auditory cortex (i.e., AI) was surrounded by a ‘belt’ area, which in turn was bordered laterally by a ‘parabelt’ region (Kosaki et al., 1997; Morel et al., 1993; Rauschecker, 1997). Whereas neurons in the core (i.e., AI) responded best to simple auditory stimuli such as pure tones, those in the belt and parabelt responded best to more complex sounds (e.g., vocalizations and bands of noise, Rauschecker et al., 1995). Most remarkably, caudal but not rostral neurons within these areas, were shown to be particularly sensitive to the location of sounds (Benson et al., 1981; Kaas and Hackett, 2000; Leinonen et al., 1980;

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Morel et al., 1993; Rauschecker, 1998; Recanzone et al., 2000; Tian et al., 2001; Vaadia et al., 1986), whereas more rostrally positioned neurons in the lateral belt and beyond were more sensitive to non-spatial acoustic qualities such as conspecific vocalizations (Rauschecker and Tian, 2000; Tian et al., 2001). Beyond auditory cortex, connections from the caudal parabelt regions were found to extend to the ventral inferior parietal (VIP) cortex of the monkey (Lewis and Van Essen, 2000) as well as reciprocally into the caudal principal sulcus (area 46) and frontal eye fields (area 8a, Hackett et al., 1999; Romanski et al., 1999a, 1999b). By comparison, the rostral belt region was found to have connections with the frontal pole (area 10), rostral principal sulcus (area 46), and ventral prefrontal areas (areas 12 and 45, Romanski and Goldman-Rakic, 2002). Taken as a whole, these results were interpreted as forming the basis of a domain-specific model of auditory processing whereby auditory non-spatial (i.e., “what”) and spatial (i.e., “where”) information were processed by ventral and dorsal brain pathways, respectively (i.e., the “what–where” model or WW model, Kaas and Hackett, 1999; Rauschecker and Tian, 2000; Romanski et al., 1999b).

This auditory model bore many similarities to the “what–where” model of the visual cortical system developed over a decade earlier in which two visual pathways were defined as emanating from the striate cortex: a ventral stream crucial for visual identification of objects, and an occipitotemporal–parietal pathway crucial for appreciating the spatial relationships among objects as well as for the visual guidance of movements towards objects in space (Ungerleider and Haxby, 1994; Ungerleider and Mishkin, 1982). Support for that model was derived from research demonstrating that lesions to monkey inferior temporal cortex resulted in deficits on pattern, object, or colour discrimination tasks, but not on visuospatial tasks such as visually guided reaching or relative distance judgments (see Ungerleider and Mishkin, 1982). Lesions to the posterior parietal cortex, on the other hand, did not seem to affect visual discrimination performance but did affect visuospatial performance. Physiological data also supported the distinction (Desimone and Ungerleider, 1989; Maunsell and Newsome, 1987), as did data from humans (Haxby et al., 1991; von Cramon and Kerkhoff, 1993).

Not long after the auditory findings in animals were reported, a similar pattern of auditory processing was revealed in humans. In one of the first experiments to offer double dissociative evidence in neurologically intact humans, we presented functional magnetic resonance imaging (fMRI) participants with noiseburst sounds that varied in pitch and perceived location (Alain et al., 2001). Relative to when listeners were asked to attend to the location features of the sounds, attention to the sounds’ pitch elicited greater blood-oxygen-level dependent (BOLD) hemodynamic activity in the auditory cortex and inferior frontal gyrus. In contrast, attending to the location properties elicited relatively greater activity in the participants’ posterior temporal lobe, superior parietal lobe and superior frontal sulcus. Event-related potentials recorded while the listeners carried out these tasks also revealed differential task effects over the anterior and posterior temporal regions. These, along with many other neuroimaging and patient observations, strongly argued in favour of a dual pathway model of human auditory cortical processing, often termed the auditory ‘what–where’ model (see Fig. 1, Ahveninen et al., 2006; Alain et al., 2008; Altmann et al., 2007; Anourova et al., 2001; Arnott et al., 2004, 2005; Barrett and Hall, 2006; Belin and Zatorre, 2000; Bushara et al., 1999; De Santis et al., 2007; Degerman et al., 2006; Deouell et al., 2007; Maeder et al., 2001; Schröger and Wolff, 1997; Tardif et al., 2008; Tata and Ward, 2005; Thiran and Clarke, 2003; Weeks et al., 1999; Zatorre et al., 2002).

Despite its popularity, the auditory WW model has not been without criticism (Belin and Zatorre, 2000; Hall, 2003; Recanzone and Cohen, 2010). One concern has been that a distinction based

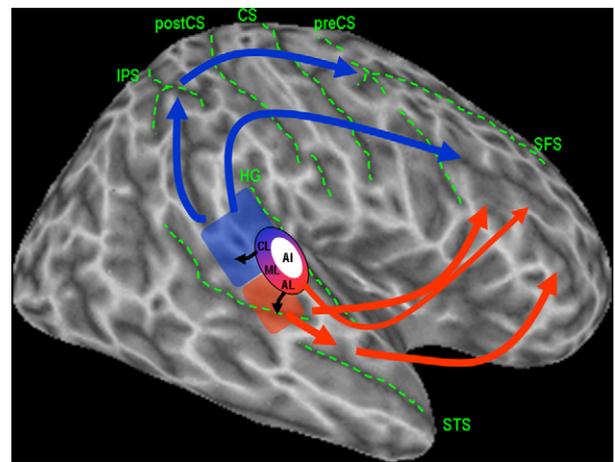


Fig. 1. Schematic of the dual-pathway model of auditory cortical processing summarizing neurophysiological and neuroimaging data from humans and animals (refer to text). The dorsal ‘spatial’ and ventral ‘what’ pathways are denoted by blue and red arrows, respectively. AI = primary auditory cortex; AL = anterolateral belt; CL = caudolateral belt; CS = central sulcus; HG = Heschl’s gyrus; IPS = intraparietal sulcus; ML = middle lateral belt; postCS = postcentral sulcus; preCS = precentral sulcus; SFS = superior frontal sulcus; STS = superior temporal sulcus. Adapted from Rauschecker and Tian (2000) and Romanski et al. (1999a).

on ‘what’ and ‘where’ features of a sound tends to be an oversimplification of the data and does not provide an adequate functional account of how the auditory system and the brain, in general, operates. Moreover, it has become apparent that non-spatial auditory processing can also elicit activation in the dorsal pathway, albeit often to a lesser extent than does spatial processing (cf. Arnott et al., 2004; Gifford and Cohen, 2005; Husain and Nachev, 2007; Renier et al., 2009), and that, in some cases, the parietal neurons that are activated by auditory spatial tasks can be the same as those activated by non-spatial tasks (Gifford and Cohen, 2005). For example, our meta-analysis of auditory neuroimaging studies demonstrated that unlike regions of the superior frontal sulcus (SFS) that were driven exclusively by auditory spatial processing, over 40% of auditory studies considered to be ‘non-spatial’ in nature (i.e., the auditory stimuli were only ever delivered from one location and the listener’s task did not involve any kind of localization or spatial judgment), reported significant functional activity in the inferior parietal lobe (IPL) region in addition to the virtually 100% of auditory ‘spatial’ processing studies that were examined (Arnott et al., 2004). Accordingly, while it is evident that the auditory dorsal pathway, and the IPL in particular, is activated any time a relative auditory spatial judgment has to be made, it is also apparent that the IPL is involved in more than just creating auditory spatial maps.

2. Re-examining the dorsal pathway

In recent years, a subtle but important variation on the role of the auditory dorsal pathway has become evident across disparate domains of auditory research. In particular, there has been an increasing emphasis on the role that the dorsal pathway plays in instructing action, or guiding motor output based on auditory information. Before reviewing these data, it is important to acknowledge the visuo-motor theory from which some of this work draws its inspiration.

Popularized in the 1990s by Milner and Goodale, the perception–action (PA) theory of cortical organization evolved out of a similar need within the visual literature to account for emerging monkey and neurological findings that the visual WW models of the time could not easily accommodate (Goodale and Milner, 1992; Milner et al., 1991). Among these was the observation that a person

could possess damage to the dorsal pathway and still exhibit some preserved spatial processing abilities. For example, it was known that optic ataxic patients with damage to the intraparietal sulcus and either the superior aspect of the IPL or the superior parietal lobule (SPL) often demonstrated difficulty reaching for or orienting their hands towards objects in the visual field, even though they were still able to accurately describe the *relative* position of objects in space (Perenin and Vighetto, 1983, 1988). Such deficits stood in stark contrast to those of a visual agnostic patient (D.F.) who, despite developing a profound visual agnosia for object form and shape following hypoxic lesions to her ventral visual pathway (that is in the lateral occipital area (LO) James et al., 2003), could still carry out skilled motor actions on those objects, implying that the dorsal stream was privy to some ‘what’ information (Goodale et al., 1991; Milner et al., 1991). In other words, lesion evidence was suggestive of a dissociation between what a viewer perceived and how a viewer acted on the visual information (i.e., instruct motor output).

Such evidence shifted the emphasis on the dual pathway distinctions from being in terms of how sensory information/input is processed (i.e., spatial versus non-spatial features) towards what the *outputs* or end result of the two streams were (i.e., one concerned with making sense of what one was seeing, and the other with acting on what one was seeing). Whereas the ventral pathway was characterized using vision to guide perception (e.g., the object lying on the table is a coffee cup), the dorsal pathway was characterized as a ‘vision-for-action’ pathway. In particular, it was the dorsal pathway that enabled the real-time control of action in such a way that enabled spatial information to be (unconsciously) transformed into the coordinate frames of the effector that was being used to carry out the action (e.g., reaching out to correctly grasp the coffee cup by the handle). To this date, the model continues to offer a robust account of visual data, in normal as well as in neurologically compromised populations (for more recent reviews, see Goodale, 2008; Milner and Goodale, 2008). Because one can readily imagine the advantages of having two systems (i.e., one that enables a person to reflect on and perceive objects in the world, and another that enables them to act on those objects with seeming effortlessness and ‘automaticity’), the model possesses a degree of intuitive appeal. More importantly, it rather nicely accommodates many visual illusion dissociations where an observer who perceives one reality (e.g., as when two lines of equal length are visually perceived to be unequal in an Ebbinghaus illusion) nevertheless behaves quite differently when asked to ‘act’ on that object (e.g., when reaching to pick up the ‘unequal’ lines, the observer’s grip aperture is correctly scaled to the object’s actual size).

2.1. Acting on auditory input

Do principles of the visuo-motor perception–action model have any relevance to audition? Increasingly, the answer to this question seems to be “yes”. Take for example two direct behavioural tests of the action–perception interpretation of auditory processing (see also, Griffiths, 2008). In one study it was demonstrated that when the pitch of a singer’s note was externally altered before it reached the singer’s own ear, that singer was found to ‘correct’ the pitch of the self-produced note even though he or she was perceptually unaware that any pitch change had taken place (Hafke, 2008). Although rigorous psychophysical research was not carried out to indicate whether the listeners were actually aware of the perceptual thresholds (and thus at some level may have been ‘perceptually aware’ of the pitch change), the results are nevertheless suggestive of an auditory perception and action dissociation. Similarly, a different research group (for similar findings see also Dalla Bella et al., 2009) found that for a given tone pair interval, persons with congenital amusia who were unable to reliably report

the perceived pitch change direction for a given interval, nevertheless were more reliably able to *reproduce* that interval when asked to hum the two tones (Loui et al., 2008). These results could also be taken as support for an auditory action stream that can operate outside of conscious awareness, and that operates separately from a conscious perceptual (or ‘what’) stream. Within the visuomotor PA model, it has been argued that while the ventral perception stream operates using relative metrics to other objects (and can therefore be encapsulated in a perceptual representation), the functions of the dorsal stream necessitate rapid coordinate computations that are capable of operating in “real-time” in order to interact with rapidly changing goal objects (Goodale, 2008). This may help explain why the dorsal system operations are not always part of conscious awareness.

Yet even apart from such direct tests, the perception–action flavour is clearly present in other areas of auditory research. Studies of rhythm perception are a good example of goal-directed action based on auditory input because in order to actively tap out a beat, one must base the timing of their action on what they are hearing. Functional brain imaging studies carried out on listeners who were asked to finger-tap to a beat typically show involvement of dorsal pathway brain areas including posterior regions of the lateral STG, as well as bilateral regions of the frontal cortex including dorsal premotor cortex, the supplementary motor area (SMA) and the pre-SMA (Chen et al., 2009; Repp, 2005). Even when naïve listeners are asked to passively attend to rhythms and not tap at all (i.e., thereby minimizing any possible ‘intent for action’), premotor, frontal and auditory areas are still recruited (Chen et al., 2009). Such findings are suggestive of an inherent link between auditory and motor systems, and therefore support a link between auditory processing in dorsal brain areas.

Apart from music and rhythm, the issue of auditory perception and action is also apparent in models of speech processing. Hickok and Poeppel in particular have proposed a dual-stream model of speech processing that is composed of a ventral auditory pathway involved in mapping sound into meaning (thereby enabling speech recognition), and a dorsal pathway that is important for mapping sound into an articulatory-based representation that enables speech perception (Hickok and Poeppel, 2000, 2004, 2007). They argue that bilateral regions of the superior temporal sulcus actively represent visuomotor correspondence between one’s own actions and the actions of others. Most recently, a review by Rauschecker and Scott (2009) outlines a similar model of speech perception and production that builds on data from Hickok as well as others. Like Hickok et al., they maintain that the postero-dorsal pathway participates in the transformation of acoustic speech signals into articulatory representations. As with our research, Rauschecker and Scott approach their theory from an auditory what–where perspective and, in so doing, argue that auditory ‘what/where’ and ‘perception/action’ theories differ mainly in point of emphasis.

2.2. Action sounds

Part of our everyday activities often includes some form of ‘action listening’. Whether it is the sound of someone walking down a hallway or a knock at the door, such sounds often deliver an immediate understanding about what that person is doing. As it turns out, research investigating how this type of auditory information is processed consistently reveals activation in the dorsal auditory pathway, even when the sounds are presented in such a way that they are devoid of any features that give rise to a spatial perception. For example, we recently demonstrated robust activation of the left IPL in participants who were performing a non-spatial auditory task that involved perceiving material properties of objects (Arnott et al., 2008). Along with control sounds, monaural audio recordings of different malleable materials being ‘crumpled’ in someone’s

hands (i.e., paper, plastic, styrofoam or aluminium foil sheets) were randomly presented in a diotic manner to each subject over headphones as they lay in an MRI categorizing each sound as being a ‘material’, ‘noise’ (i.e., scrambled material sound file) or a non-verbal ‘human’ sound (e.g., coughing and snoring). Interestingly, while we confirmed our hypothesis that auditory material-specific activity would be found in an area of the brain that we believe is involved in the perception of the surface properties of an object (i.e., posterior ventromedial brain regions, Cant et al., 2009; Cant and Goodale, 2007), we also found very reliable non-spatial, auditory material-specific activation in the left IPL along the inferior parietal sulcus. This region was just posterior to the human homologue of the anterior intraparietal area (hAIP), roughly corresponding to the vicinity of the caudal intraparietal area (CIP). While the former has been well-documented in macaques to be involved in visually guided grasping movements towards objects (for a review, see Culham et al., 2006), area CIP is known to be activated during the visual analysis of surface and pattern orientation, especially as it relates to reaching or grasping objects (Grefkes and Fink, 2005; Shikata et al., 1996; Taira et al., 2001). As there was no spatial processing required in this diotic sound material identification task, the activation could be interpreted as reflecting the use of action-schema by the listeners in order to identify the sound as a material (i.e., imagining the action of crumpling a sheet of material with one’s hand in response to hearing the sound). Post-experimental debriefings revealed that these naïve participants all reported having the (accurate) impression that the sounds were created by having someone ‘crumple’ various pieces of material in their hands.

Although that ‘material sound’ study was not specifically designed to investigate the ‘action’ nature inherent in those sounds, studies that have been designed for that purpose reveal similar brain activations. For instance, Lewis and colleagues also reported activation of the left IPL when right-handed participants listened to the nonspatial sounds of hand tools (e.g., drills) being appropriately used as compared to when they listened to animal sounds (Lewis et al., 2005, 2006). Lewis et al.’s interpretation of the activation patterns was essentially an action-schema account that involved the “mental mimicry of motor production sequences” that were most likely to have produced the sounds (see also Lewis et al., 2004). Finally, another fMRI study in human listeners also revealed that the processing of ‘action sounds’ activated the intraparietal sulcus (Lahav et al., 2007). In that study, non-musicians were first trained on a piano to play a particular piece of music by ear. Later, when these participants were presented with the same piece of music while their BOLD activity was recorded with fMRI, bilateral activation was found in regions of the frontoparietal motor network that included, in addition to the intraparietal area, the inferior parietal area, premotor region, and Broca’s area. Importantly, during the presentation of the music, the listener’s task did not involve performing any movements, but merely involved listening to the music. In keeping with an auditory-based action processing account, such brain activity was greatly attenuated when the order of the musical notes was altered and, in fact, was not observed at all when the same participants listened to an equally familiar, but motorically unknown piece of music.

3. Sound localization: calls to action?

“Look with thine ears” – Act 4. Scene VI, King Lear, William Shakespeare

Given the wide range of evidence outlined above implicating dorsal brain regions as being involved in auditory-motor integration, it may be useful to consider spatial localization and the ‘where’ pathway from an auditory-motor perspective. In their paper, Kubovy and Van Valkenburg (2001) argued that auditory

spatial localization system could be thought of as one that was “in the service” of visual orientation and that the major function of auditory localization was to direct the eyes to a location of interest. As they stated, such a notion was itself a more refined version of a long-held belief by James Angell approximately a century earlier that people seem to make their localization of sounds either in the form of visual imagery, or in the form of quasi-reflexive movements of the head and eye (Angell, 1908). In the current section, we will present evidence in support of this claim. Before continuing however, an overview of the neural circuitry controlling eye movements is offered.

3.1. Cortical areas involved in the generation of saccades

The large amount of research that has been devoted to the study of eye movements has provided a reasonably good understanding of the neural circuitry underlying saccade generation. For the purposes of the present paper, our overview of saccadic circuitry will focus on the parietal and frontal cortical areas (summarized in Fig. 2), although nodes within the cingulate gyrus, caudate, cerebellum and brain stem also exist. Further details can be found in more formal reviews (e.g., McDowell et al., 2008; Munoz et al., 2000; Pierrot-Deseilligny et al., 2004). What is important to note throughout, however, is the degree of overlap between areas activated by auditory spatial processing, and those involved in the generation of eye movements.

Saccades can be broadly classified into two types: reflexive and volitional. Reflexive (also referred to as prosaccades) are those made immediately to the appearance of peripheral visual stimuli. Reflexive saccades are generated via projections from the posterior parietal cortex to the superior colliculus, with the latter subcortical structure being chiefly responsible for the actual execution of any type of saccadic movement (Gaymard et al., 2003; Pierrot-Deseilligny et al., 2004). The region of posterior parietal cortex known to be chiefly involved in reflexive saccades is referred to as the parietal eye field (PEF). Its precise location is equivocal, with some research placing it in the dorsal portion of the inferior parietal lobe, on the lateral aspect of the IPS (Müri et al., 1996; Pierrot-Deseilligny et al., 2004), while others claim a more medial position (Koyama et al., 2004). Strong stimulation of the corresponding area in monkeys (i.e., the lateral intraparietal (LIP) area) elicits contralateral saccades whereas weak stimulation elicits a contralateral visual attention shift (Cutrell and Marrocco, 2002). This latter finding also underscores the role that the PEF plays in attentional processes (Bisley and Goldberg, 2003; Wardak et al., 2002). More recently, a frontal lobe contribution to reflexive eye movements has also been established with a diffusion tensor imaging (DTI) study revealing that the lateral premotor area projects to the IPL, whereas the medial premotor area has connections with the SPL, DLPFC and cingulate gyrus (Tomassini et al., 2007). In light of the frontal lobe’s role in saccadic inhibition (Munoz, 2002), such connections may reflect, in part, a means of modulating saccades or at least shifting visual attention.

Though reflexive saccades account for a good proportion of eye movements, another type of saccade includes those that are not immediate responses to an external event, but are either delayed or occur as a result of the observer’s own desire. These volitional saccades may occur when the observer is already attending to one object or task and must inhibit a (reflexive) saccade to the occurrence of a secondary visual stimulus in the periphery, until the time is appropriate. In other cases, a volitional saccade may be initiated out of a desire to explore the visual environment. Unlike the PEF-driven reflexive saccades, volitional saccades appear to be more dependent on contributions from the frontal lobe (Pierrot-Deseilligny et al., 2004). In fact, human research involving memory-guided saccades consistently demonstrates the

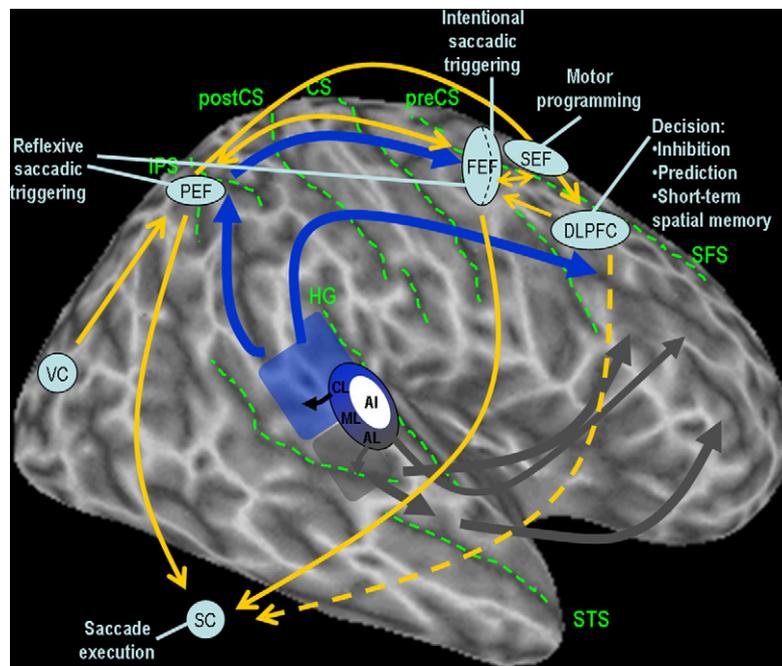


Fig. 2. Schematic of cortical areas involved in eye movement programming (adapted from Pierrot-Deseilligny et al., 2004) overlaid on the auditory dual-pathway schematic from Fig. 1 (dorsal pathway in blue, ventral pathway in gray). Dashed yellow line represents inhibitory connections. AI=primary auditory cortex; AL=anterolateral belt; CL=caudolateral belt; CS=central sulcus; DLPFC=dorsolateral prefrontal cortex; FEF=frontal eye field; HG=Heschl's gyrus; IPS=intraparietal sulcus; ML=middle lateral belt; PEF=parietal eye field; postCS=postcentral sulcus; preCS=precentral sulcus; SC=superior colliculus; SEF=supplementary eye field; SFS=superior frontal sulcus; STS=superior temporal sulcus; VC=visual cortex.

involvement of a premotor region in the vicinity of the precentral sulcus and the caudal-most portion of the SFS, known as the frontal eye fields (FEFs; Brown et al., 2004; Camchong et al., 2006; Paus, 1996; Srimal and Curtis, 2008). This region has long been implicated as a principal brain area involved in oculomotor control given its role in the initiation of voluntary saccadic and pursuit eye movements (Bruce et al., 1985; Paus, 1996).

For example, studies that adopt ocular motor delayed response tasks in which participants are instructed to remember the location of a peripherally presented visual target over the length of a given time period and then generate a saccade to that unmarked location after the delay, often incite activity in the frontal (as well as the parietal) lobe, over and above the basic saccadic circuitry that is already enacted (see, McDowell et al., 2008). Part of the activity in the FEF may reflect memory-guided maintenance of the task's response requirements (Curtis and D'Esposito, 2006) by coding the spatial location of the cue (Srimal and Curtis, 2008). Furthermore, left FEF activity has been implicated in the maintenance of a cue's location whereas right FEF activity has been associated with the preparation and/or planning of a response in addition to maintaining location (Geier et al., 2007). This latter study also found that like the right FEF, activity in the supplementary eye fields (SEFs) located in the upper part of the superior frontal gyrus and on the medial surface of the SFS (Grosbras et al., 1999), was also related to response preparation and/or planning. In general, SEF activity is thought to relate to the motor programming involved in combining a saccade with another body movement, as well as the programming of a sequence of successive saccades (Pierrot-Deseilligny et al., 2004).

In addition to FEF and SEF regions of the frontal lobe, the DLPFC has also been implicated in volitional saccadic programming, especially as it pertains to the maintenance of spatial information in order to mnemonically (Constantinidis et al., 2001) guide the eventual eye saccade (D'Esposito et al., 2000; Funahashi et al., 1993; Geier et al., 2007; Postle et al., 2000), as well as with respect to its involvement in inhibiting reflexive saccades (Camchong et al.,

2006; Ford et al., 2005). Consistent with the latter point, McDowell et al. (2005) examined the response-locked activity associated with reflexive saccades and volitional saccades made in the direction opposite to the visual event. An examination of the inhibitory activity as revealed by contrasting antisaccade with the prosaccade activity showed, in addition to greater activity in the DLPFC, increased activation in the medial FEF, SEF and prefrontal cortex, again supporting the general notion of a frontal lobe source for inhibitory saccadic commands (Munoz, 2002).

3.2. Eye movements as an ecologically valid response to auditory localization

With a basic understanding of the saccadic circuitry, we will now review research demonstrating the close functional relationship between auditory spatial localization and visual processes. Although this review focuses predominately on eye movements as a means of orienting the visual system, head- and body-orienting behaviours could also be included in this. The relevance of these behaviours to successful sound localization is not lost on the observation that cats, monkeys, and humans all tend to localize sounds more poorly when their heads are restrained and unable to make orientation movements (Populin, 2006, 2008; Tollin et al., 2005). From a functional imaging perspective however, the relatively small amount of muscle and body motion incurred by eye movements relative to other types of visual orientation makes saccades a more appropriate method for study.

In the past, many studies of auditory spatial processing, including the majority reviewed in Section 1, have tended to ignore or downplay the role of eye movements (see, Populin, 2008) by emphasizing non-visuomotor processes, employing auditory spatial tasks where listeners passively attend to the location of a sound (Griffiths et al., 1994, 2000; Griffiths and Green, 1999) or utilizing categorization tasks while the sounds emanate from various locations (Butler et al., 1990; Weeks et al., 1999, 2000; Zatorre et al., 1999). Still other studies have had listeners indicate particular

'target' or 'oddball' locations with a button press (Alain et al., 2008; Barrett and Hall, 2006; Iacoboni et al., 1998), or perform a self-report or comparison task about a sound's location (Alain et al., 2001; Altmann et al., 2008; Grady et al., 2008; Martinkauppi et al., 2000; Wightman and Kistler, 1989). Finally, even when more ecologically relevant approaches to sound localization have been employed such as the use of head-pointing (Carlile et al., 1999; Makous and Middlebrooks, 1990; Recanzone and Makhamra, 1998), or pointing with tools like a gun, stylus, joystick or laser beam (Bushara et al., 1999; Gilkey and Anderson, 1995; Langendijk et al., 2001; Lewald and Ehrenstein, 1998; Oldfield and Parker, 1984; Zwiers et al., 2003), eye movements have been largely ignored.

Yet, in most real-life situations, the process of sound localization usually acts in concert with eye movements. Heffner and Heffner (1992) have made an especially compelling case for this relationship by quantitatively demonstrating that across vertebrate species, the most reliable predictor of sound localization ability is not whether the animal is predominately prey or predator, diurnal or nocturnal, or has a small or large head (an attribute that directly relates to the ability to use binaural cues), but rather the extent of their field of 'best' vision (Heffner and Heffner, 1992). Specifically, animals that have relatively narrow visual fields (e.g., humans and elephants) have good sound-localization acuity, whereas those with wide visual fields do not (e.g., spiny mouse and horses). The correlation is quite striking ($r=0.89$, Heffner and Heffner, 1992) and has been shown to hold true not only within a given taxonomic order (e.g., chiroptera (bats), Heffner et al., 2007), but more importantly, regardless of overall visual acuity. These data also make the point that even animals with very poor visual acuity will still orient what little vision they have (i.e., their 'best' vision) towards a sound source. Much of this likely has to do with the fact that foveal vision offers more reliable and far more detailed information about a given object than does auditory information (Alais and Burr, 2004; Witten and Knudsen, 2005).

Furthermore, there is a well-known eccentricity effect with respect to saccades in which saccadic reaction times (SRTs) to auditory events *decrease* as a function of increasing target eccentricity, whereas SRTs increase in response to visual events at increasing eccentricities (Cohen and Ross, 1977; Frens and Van Opstal, 1995; Gabriel et al., 2010; Lueck et al., 1990; Zambanieri et al., 1982). Specifically, saccades to centrally located stimuli (i.e., $<10^\circ$ from fixation) tend to be faster for visual relative to auditory events, but for distances greater than 10° horizontal eccentricity, the SRT relationship reverses and auditory-guided saccades become increasingly faster than visually-guided saccades (Frens and Van Opstal, 1995; Gabriel et al., 2010) to the point that sounds located outside of central vision are localized as fast as saccades to visual events located just a few degrees from central fixation (Frens and Van Opstal, 1995). Accordingly, depending on whether visual or auditory information is used to guide saccades to locations along the horizontal meridian, these data suggest that it is possible to maintain a relatively constant SRT to objects in the environment.

Further evidence for the interaction between visual and auditory spatial processes is that eye movements and eye position can alter auditory spatial perception. For example, after a person has been tracking moving objects for a period of time (as occurs when observing individual telephone poles on the side of the road from a travelling car; optokinetic nystagmus), reflexive eye movements to brief auditory targets are often shifted in the direction of the tracking movements (Konigs et al., 2007). In addition, auditory space has been shown to 'shift' as much as 40% in the direction of a sustained fixation point, presumably as a means of realigning auditory and visual spatial maps in terms of "straight-ahead" (Cui et al., 2008; Razavi et al., 2007), results echoed by eccentric gaze effects on the localization of both auditory and visual stimuli (Cui et al., 2010; Lewald, 1997, 1998; Otake et al., 2007;

Van Barneveld and John Van Opstal, 2010). Consistent with this, Zimmer et al. (2004) have reported V1/V2 hemodynamic activity associated with sound localization that occurs during eccentric eye positions in neurologically intact persons, suggesting a relation between neural processing in the visual cortex and the transformation of auditory spatial coordinates responsible for maintaining the perceptual alignment of audition and vision with changes in gaze direction.

Eccentric eye position exerts its effects on neurons at a number of different levels in the auditory pathway, including the superior colliculus (Jay and Sparks, 1984, 1987), and the spatially sensitive neurons of the caudal belt (Woods et al., 2006). Furthermore, saccadic trajectories towards visual stimuli can be altered by the presence of non-informative auditory distractors (Doyle and Walker, 2002; Sheliga et al., 1994, 1995), and visual spatial judgments can be altered by the presence of localized auditory events (Arnott and Goodale, 2006). Even the costs associated with invalidly cued auditory localization judgments have been found to be reduced when repetitive transcranial magnetic stimulation is applied to the FEF (Smith et al., 2009), suggesting that even during normal auditory spatial attention, the eye-movement system is involved. Finally, perhaps one of the most convincing examples of an auditory spatial link to the visual orientation system comes from Zwiener et al.'s (2003) adaptation study. Auditory localization measures carried out on participants who had worn lenses for 2–3 days that compressed the visual field by a factor of 0.5, not only demonstrated a corresponding compression of the auditory field within the visual field of view, but also showed that the localization of peripheral auditory locations that were outside the visual field of view (and thus had not been subjected to visual-auditory distortions) was also affected.

All of this serves to underscore that auditory spatial processing and the eye movement system are not processed in strictly isolated and independent manners. Rather, the localization of auditory events often interacts and integrates with the visual system. Prior research comparing auditory and visual spatial networks in neurologically intact humans has tended to show both distinct activations (e.g., within auditory and visual cortices) as well as common areas of functional overlap (e.g., within prefrontal and parietal regions, Bushara et al., 1999; Lewis et al., 2000; Martinkauppi et al., 2000; Sestieri et al., 2006; Stevens et al., 2000). However, it is often unclear from this earlier work the extent to which the overlapping auditory and visual networks reflect spatial processing *per se*, or are related to arousal, task demands and/or response-related activity (e.g., button pressing). For example, Bushara et al. (1999) found modality-specific activation within distinct areas of the SPL as well as the middle frontal gyri when comparing functional activity associated with an auditory localization task and a visual localization task. Common areas of overlap between modalities included bilateral IPL, right inferior temporal cortex and right medial frontal cortex. This region of the parietal lobe was also found to be active during a crossmodal spatial localization task (Sestieri et al., 2006). Specifically, when participants performed a location matching task based on visual objects that were presented in the left or right hemisphere and that were paired with corresponding environmental sounds presented to the left or right ear, location-specific activity was found within the right intraparietal sulcus. Taken together, these results suggest that the region around the intraparietal sulcus (including the IPL and SPL) shows both overlap and modality-specific activation during spatial tasks. Such activity does not seem to be related to the task-related response measures (i.e., response button pressing), since this activity was over and above that associated with non-spatial tasks that required similar motor responses (see also Alain et al., 2008). However, given the proximity to the PEFs (see Section 3.1), the possibility

remains that some of this activity could relate to eye movement programming.

3.3. Cortical brain regions where auditory–visual spatial interactions occur

Although there is no doubt that subcortical structures such as the superior colliculus play a significant role in integrating auditory space with visual information and eye movements (Jay and Sparks, 1984, 1987; Lomber et al., 2001; Maier and Groh, 2009; Meredith and Stein, 1983; Wallace et al., 1996), there is equally little doubt of the involvement of cortical structures in this behaviour (Alvarado et al., 2007; Stricanne et al., 1996). It is this latter involvement that we will turn to now.

3.3.1. Frontal eye fields

Research in the macaque demonstrates that whereas the lateral FEF is innervated by visual afferents from retinotopically organized foveal representations and areas that represent central vision in inferotemporal cortex, the medial FEF receives input from auditory areas as well as retinotopically organized peripheral representations and other areas emphasising peripheral vision (Schall et al., 1995). Consistent with the notion that auditory localization serves to orient the visual system to peripheral locations of interest, lateral and medial FEF are known to code for short and long saccades, respectively (Schall et al., 1995). Given that visually and aurally responsive FEF neurons are active both before and during saccadic execution (Mohler et al., 1973; Russo and Bruce, 1994), it seems plausible that auditory spatial processing may automatically prime the FEFs to prepare volitional eye movements or at least direct attention to an auditory event. These qualities are certainly in keeping with our finding that auditory spatial (but not non-spatial) processing is associated with activation in regions around the SFS (Arnott et al., 2004). Notwithstanding the fact that none of those auditory spatial studies actually involved eye movements (indeed, some actively discouraged it, potentially accounting for DLPFC activity related to saccadic suppression), it has been shown that neurons within the FEF participate not only in volitional eye movements, but also in overt as well as covert shifts of attention to particular locations in space (Schall, 2004).

With respect to non-eye movement related activity, single cell evidence in monkeys demonstrates that some FEF neurons code for the spatial location of objects, even in the absence of saccadic preparation (Armstrong et al., 2009). Interestingly, recent evidence suggests that the FEF can be activated very quickly following the onset of external stimuli. For example, using human intracerebral recordings it was demonstrated that FEF activity was modulated as early as 45 ms following the onset of a visual stimulus, and as early as 24 ms following the onset of an auditory stimulus (Kirchner et al., 2009). Direct projections from auditory cortex to the FEF appear to support this rapid time course (Hackett et al., 1999). In this manner, the FEF may be viewed as part of a direct route for rapid activation of circuits serving multimodal spatial attention (Muggleton et al., 2009; Nuding et al., 2009; Ungerleider et al., 2008). Moreover, this FEF coding does not appear to be restricted to ‘visual’ space. Although some of the early FEF findings reviewed above (cf., Goldberg and Bruce, 1990; Russo and Bruce, 1993; Schall et al., 1995) have traditionally been interpreted to suggest that the FEF represents space retinotopically, more recent studies have begun to show otherwise. A functional imaging investigation of human subjects carrying out an auditory localization working memory study (Tark and Curtis, 2009) revealed that FEF activity was present not only for stimuli occurring in retinal space, but also for auditory sources located behind the head (i.e., in ‘extra-retinal’ space). Such results suggest the existence of FEF neurons that represent space in a head-centred (i.e., auditory-space) or hybrid coordinate frame.

3.3.2. Parietal lobe

Auditory and visual signals are known to converge in many areas of the primate parietal lobe including the lateral, medial, and ventral banks, and regions within the intraparietal cortex likely play a role in guiding attention to, remembering and responding to locations of sensory stimuli (Andersen and Buneo, 2002; Colby and Goldberg, 1999). Furthermore, the parietal cortex is almost always reported active during tasks that require sound and/or visual localization (Arnott et al., 2004; Ungerleider and Haxby, 1994), with activity in the right IPL predicting behavioural performance on auditory spatial localization tasks (Leung and Alain, 2011; Zatorre et al., 2002). Auditory and visual information may preferentially activate different areas of parietal cortex, with one fMRI study that measured orienting and maintenance of auditory and visual spatial attention finding that inferior and superior parietal lobules were more activated by auditory and visual spatial tasks, respectively (Salmi et al., 2007). The fact that such activation seems to occur only when explicit attention is devoted to spatial stimuli (Tiitinen et al., 2006; Zatorre et al., 2002), suggests a role for the parietal cortex in active attentional tasks. In keeping with this, results from our own lab demonstrate that even when response-related (i.e., button press) activity is accounted for in the cortical functional activity associated (by modelling the target-related activity associated with the button press response to an auditory location repetition), sustained sound localization activity persists in the parietal lobe and is even modulated by the difficulty of the working memory task (Alain et al., 2008, 2010).

That said, a pervasive role that has been attributed to parietal cortex is that involved in sensorimotor integration. Indeed, the above results are not inconsistent with a role of the parietal cortex in preparing eye movements to those auditory locations, especially with respect to the PEF. In both monkey and human parietal cortex, there exist neurons that have retinotopic receptive fields that show preferred tuning to contralateral space, and that show spatially tuned elevated firing rates during delay periods prior to making saccadic responses (Blatt et al., 1990; Gnadt and Andersen, 1988; Schluppeck et al., 2006). Whether this type of activity reflects retrospective stimulus representation or goal-directed activity is a matter of debate (Gottlieb, 2002). In addition to eye movement planning, regions of the posterior parietal cortex are dedicated to planning other types of movements, including reaching and grasping (Andersen, 1997).

What is the nature of this sensorimotor parietal activity? A good deal of research indicates that the parietal cortex translates the location of an auditory object into a coordinate system that can be used in conjunction with the visual system (Stricanne et al., 1996). Recent research shows that neurons activated during saccades to sounds or visual events appear to operate on a reference frame that is neither purely head- (i.e., auditory) nor eye-centred but rather is a ‘hybrid’ version of both (Gherri et al., 2008). Furthermore, monkey and human research on the ventriloquism after-effect suggests that this hybrid reference frame can be spatially specific in that the recalibration of auditory space that occurs following adaptation to audio–visual stimuli only occurs for locations around the trained spatial region (Kopco et al., 2009). In other words, the parietal cortex may provide a supramodal map of an object’s location that can be used to guide behaviour and response to task-relevant stimuli (but for evidence against a single, modality-independent spatial representation of sensory signals, see Klingenhoefer and Bremmer, 2009). This modality-invariant representation of space is also supported by the fact that ventral intraparietal neurons in the macaque respond with varying intensity according, not only to the spatial location of sounds, but also preferentially to visual stimuli occurring at the same location as those sounds (Schlack et al., 2005). This work also makes it clear that the posterior parietal cortex is a heteromodal region of sensory convergence where multisensory

integration and coordinate transformation occurs (Macaluso and Driver, 2005).

3.3.3. Other cortical regions

Studies examining auditory spatial processing as it relates to eye position have found non-systematic effects localized to the spatially sensitive neurons of the caudal belt (Woods et al., 2006). Furthermore, electrophysiological investigations of macaque auditory cortex suggest that the eccentric eye effects in the temporal lobe may originate from feedback projections from parietal or frontal cortices as opposed to subcortical structures (Fu et al., 2004), and that the caudal portion of the auditory belt and parabelt regions provide the bulk of auditory connections related to directing eye movements towards stimuli of interest (Hackett et al., 1999).

With respect to visual cortex, accumulating evidence suggests the region is also modulated by sound localization tasks. Some of this research includes the finding that the hemodynamic activity in human visual cortex increases when listeners localize sounds without making any eye movements (Zimmer et al., 2004), that peripheral visual cortex is activated by sound sources outside the visual field (Cate et al., 2009), and that sound localization is systematically shifted when repetitive transcranial magnetic stimulation (rTMS) is applied over occipital cortex (Lewald et al., 2004). Moreover, 'retinotopic' distortions of visual space using peripheral visual cues have also been found using peripheral auditory cues (Arnott and Goodale, 2006), and the superior auditory spatial processing abilities exhibited by cortically blind individuals often stems from the recruitment of occipital areas (Collignon et al., 2009). As with the FEF, modulations in visual cortical activity as a result of auditory events are made plausible by the direct long range connections that exist between the occipital and auditory cortices (Clavagnier et al., 2004; Falchier et al., 2002; Hikosaka et al., 1988).

3.4. Summary

In an effort to understand auditory spatial processing in the context of a dorsal pathway that is useful for guiding motor output in order to achieve goal-directed outcomes, we have reviewed evidence showing the close interface between auditory spatial processing and visual processes, especially as it relates to guiding the oculomotor system towards locations of interest. In this way, it may be possible to understand auditory spatial processing (and thus the dorsal auditory pathway) as being related to the programming of saccadic movements towards a location in space.

In keeping with this, part of the contribution of the parietal lobe seems to be to compute a supramodal map of space in order to carry out sensorimotor integration tasks that can lend itself to guiding eye movements (or reaching and grasping movements) to a particular location. With respect to the frontal lobe, physiological research suggests that particular regions of the FEF receive direct input from auditory and peripheral visual areas, and that these FEF regions are activated very early following the onset of a stimulus (visual or auditory). In addition to its role in directing volitional eye movements, the FEF may be particularly relevant for directing attention to regions of space that are not only outside the central visual field, but are outside the visual space entirely. In the final section, we will consider the auditory dorsal stream in a larger, multimodal context by considering the role that attention plays in orienting the visual system to a sound of interest.

4. Dorsal pathway and attentional orienting

In addition to its role in eye movement programming, it is clear from what we have reviewed that a large proportion of auditory activity in the dorsal stream is associated with attentional processing. The inclusion of an attentional component does not invalidate the idea that auditory localization serves to inform/orient the visual

system. In reality, spatial attention and eye movement programming can be thought of as part and parcel of the same orienting mechanism. For instance, while strong stimulation of the PEFs in monkey area LIP results in overt eye shifts to contralateral space, weak stimulation of the same area results in *attentional* shifts to that contralateral space (Cutrell and Marrocco, 2002). In other words, overt visual orienting mechanisms (i.e., eye movements) can be regarded as occupying one end of an orientation continuum. As such, spatial shifts of attention can be regarded as a form of orientation that is either low-level (e.g., a precursor to eye movement itself), or perhaps a covert way of monitoring a spatial location without involving overt orientation movements of the head, eyes, or entire body. One can certainly imagine situations in which the ability to suppress overt eye movements and merely attend to a particular spatial location without drawing attention through body motion would be functionally advantageous to an organism. As such, the dorsal pathway seems well suited for directing this type of behaviour.

The idea that the dorsal stream is important for attentional orienting has been advanced as a reason why the dual pathway functional specialization in vision exists in the first place. For example, Vidyasagar (1999) has argued that, in the case of visual search tasks, the dorsal pathway's sensitivity to movement and low contrast stimuli make it well suited for directing the focus of attention to various locations where the colour-sensitive and spatially detailed processing of the ventral pathway can be deployed. In effect, the dorsal pathway functions as a kind of filter that directs the 'attentional spotlight' to particular regions in space so that ventral stream processes can be brought to bear on the objects/features at that location. In a similar manner, Bar et al. (2006) have argued that through 'bottom-up' and 'top-down' interactions, a faster dorsal pathway may provide an earlier, coarse representation of visual objects that can, in turn, be used to inform and/or bias ventral pathway processes.

Although these theories were based on visual research, they certainly have relevance to the auditory domain, especially in light of the repeated findings that the auditory dorsal 'where' stream appears to process information more quickly than does the ventral 'what' stream. For instance, an early behavioural study by Näätänen et al. (1980) demonstrated that listeners were faster to detect changes in a tone's location (left or right ear) compared to large (>7000 Hz) changes in frequency. Moreover, several functional imaging results also support this finding (but see, Woods et al., 2001), including an electrophysiological study in macaques that found a temporal advantage for the visual dorsal over the ventral stream (Chen et al., 2007). For example, Schröger and Wolff (1997) found that location deviations (i.e., 300 μ s interaural timing differences) in a tonal pattern generated a mismatch negativity component (MMN) that was 25 ms earlier than the MMN elicited by frequency deviations (600 Hz versus 660 Hz) in the tonal pattern, even though the two types of deviations were shown to be equally salient. Similarly, during a passive listening experiment, changes in the location of animal vocalizations (i.e., 90° left or right of midline as simulated by generic HRTFs) were found to elicit neural activity that was 100 ms earlier than that elicited by changes in the type of animal vocalization (i.e., sheep call or barking dog, Altmann et al., 2007). Moreover, the locations where these changes took place occurred along regions in the 'where' and 'what' pathways, respectively. Finally, Ahveninen et al. (2006) also reported auditory evoked potential activity related to localization processing (45° left versus 45° right locations as determined using HRTFs) that was 30 ms earlier than that related to identification processing (vowel discrimination). As in the Altmann study, fMRI revealed that the location of these changes occurred in respective what-where pathways. While these findings suggest that the auditory dorsal pathway's processing speed is such that it could begin to facilitate

visual orienting mechanisms before ventral processes had even finished, they also highlight the obvious, but heretofore understated notion that sound localization serves to inform and orient the auditory system itself. That is, while auditory localization may be ‘in the service’ of the visual orienting system, it surely contributes to the auditory system as well, by directing the ventral stream processes to particular sound sources or objects (Arnott and Alain, 2002; McDonald and Alain, 2005).

4.1. Multiple streams

That said, how can an action schema involving eye movements or attentional shifts to particular locations explain IPL activations in response to sounds that have no apparent spatial properties (cf., Arnott et al., 2004)? One possibility is that by processing non-spatial and spatial information, the IPL is able to form a more stable/salient perceptual representation of an object in order to guide goal-directed behaviour (Cohen et al., 2005). This interpretation is consistent with the previously reported findings of increased IPL activity in response to non-spatial action sounds (Arnott et al., 2008; Lewis et al., 2005, 2006), with the argument being that by associating the auditory action sounds with those objects, the listener is able to acquire a more vivid or stable percept of the object in question. Indeed, these arguments echo earlier sentiments that a major function of the dorsal pathway is to direct attention to objects (Corbetta and Shulman, 2002; Vidyaasagar, 1999).

Even with the inclusion of an attentional component, we acknowledge that viewing the auditory dorsal stream as one that directs the visual system to a location of interest may not explain all instances of auditory spatial function. Rather, it is possible that multiple processes are being carried out in the dorsal pathway and that a single rubric will never capture the entire functional aspects of this region of the brain. Indeed, as Kaas and Hackett (1999) noted in their original commentary on the auditory dual pathway data, there may in fact be multiple streamlets in the auditory dorsal pathway. We would note too that a major difference between visual and auditory spatial processing is that visual objects can be gleaned from the retinotopic organization of the visual system. Since no such topographic map of auditory space has been found in the human cortex, there is a real need within the auditory system to incorporate auditory processing into some form of spatial map. While some of this computation is carried out in subcortical structures like the superior colliculus (Jay and Sparks, 1987), regions of the dorsal pathway are most likely also involved, especially in the parietal cortex as we have seen (Andersen, 1997; Bushara et al., 1999; Lewald et al., 2002; Stricanne et al., 1996). Accordingly, another streamlet within the dorsal pathway may be one that is separate from a potential orienting stream. Indeed, Corbetta and Shulman (2002) have long argued in favour of a two-system model of dorsal stream function with one involved in directing attention towards behaviourally relevant events, and the other being involved in the reorienting of spatial attention to salient and unexpected events. Given the broad role that the parietal cortex plays in auditory processing, including spatial representation, spatial attention, eye movement (motor) planning, sensory motor integration and goal-directed action (Andersen et al., 1997; Cohen, 2009), the likelihood of multiple dorsal streams or functions coexisting within the auditory dorsal pathway remains plausible.

5. Concluding remarks

Viewing the auditory dorsal pathway as one that guides or instructs motor output based on acoustic information offers certain advantages. As has been shown, it rather nicely encapsulates models of speech processing (Hickok and Poeppel, 2007;

Rauschecker and Scott, 2009), and helps explain why non-spatial sound processing can stimulate activation in dorsal areas. In keeping with the notion of goal-directed actions, our literature review has shown how auditory spatial processing within the dorsal pathway may be thought of as a means by which the visual system can be guided to a peripheral location of interest. Although the predominate method by which this occurs is in terms of overt orientation movements of the body (e.g., eye movements), one can also include shifts of attention since such shifts are often part and parcel of orientation movements (and indeed can occur in lieu of such movements). In addition, incorporating an action-based schema into the view of the dorsal auditory pathway does not necessarily discount the possibility that non-spatial auditory events can elicit activity in the dorsal pathway, in the sense that such information may enhance the goal-directed output. Finally, although we suggest that an action schema may be helpful in providing a more holistic account of dorsal auditory function, it is acknowledged that other processes may be occurring in dorsal pathway that are not immediately relevant to motor-output (cf., Husain and Nachev, 2007). Accordingly, we suggest that an aspect of auditory research that should be more fully investigated in the future, is aimed at dissociating possible contribution of eye movements to auditory spatial processing.

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