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Eye-movements intervening between two successive sounds disrupt comparisons of auditory location

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Summary

Many studies have investigated how saccades may affect the internal representation of visual locations across eye-movements. Here we studied instead whether eye-movements can affect auditory spatial cognition. In two experiments, participants judged the relative azimuth (same/different) of two successive sounds presented from a horizontal array of loudspeakers, separated by a 2.5 secs delay. Eye-position was either held constant throughout the trial (being directed in a fixed manner to the far left or right of the loudspeaker array), or had to be shifted to the opposite side of the array during the retention delay between the two sounds, after the first sound but before the second. Loudspeakers were either visible (Experiment 1) or occluded from sight (Experiment 2). In both cases, shifting eye-position during the silent delay-period affected auditory performance in the successive auditory comparison task, even though the auditory inputs to be judged were equivalent. Sensitivity (d') for the auditory discrimination was disrupted, specifically when the second sound shifted in the opposite direction to the intervening eye-movement with respect to the first sound. These results indicate that eye-movements affect internal representation of auditory location.

Keywords

auditory space perception; eye-movements; spatial cognition

Introduction

The ability to localise sounds in space is crucial for many aspects of cognition and behaviour. In addition to purely auditory tasks, accurate sound-localisation can also enhance responses to visual scenes via multisensory integration (e.g., Stein & Meredith, 1993; Knudsen & Brainard, 1995; Calvert, Spence & Stein, 2004; Spence & Driver, 2004). For instance, it can allow orienting towards events that might otherwise go undetected (e.g. outside the current field of view). However, constructing stable representations of auditory space while we act in a multisensory environment may pose some challenges for the brain. Soundwaves are affected by the head and external parts of the ears, giving rise to the well-known localization cues of inter-aural intensity and timing differences, plus spectral cues (Blauert, 1997). Changes of head-position are common in daily life, and will affect such auditory localization cues. But here we consider whether changes of just eye-position may also need to be considered for auditory spatial cognition. While there is some considerable

previous work on how eye-deviation *per se*, in one static direction or another, may affect reports of auditory location (e.g. Weerts and Turlow, 1971; Lackner, 1973; Lewald and Ehrenstein, 1996a, 1996b; Lewald, 1997, 1998), to our knowledge there has been rather less study of how shifts of eye-position (rather than fixed eye deviations) may affect auditory spatial cognition (though see Vliegen, Van Grootel & Van Opstal, 2004; Kopinska and Harris, 2003, as discussed later below).

While eye-movements *per se* will obviously not alter auditory input, they will change or 'remap' the spatial alignment between an auditory source and retinal visual information (Pöppel, 1973). Such spatial alignment can be important for stable multisensory space perception (e.g., Knudsen & Brainard, 1995; Spence & Driver, 2004). Moreover, there is now abundant evidence from neuroscience that visual locations may be remapped, in eye-centric terms, during retention delays without stimulation in which saccades intervene (e.g., Merriam, Genovese & Colby, 2003, 2007; Bellebaum, Hoffmann & Daum, 2005; Nakamura & Colby, 2002). Here we examine whether eye-position shifts during an intervening delay can also affect auditory performance, in a perceptual comparison task (same/different azimuth) for two successive sounds across a delay.

Some effects of static eye-direction (i.e. nondynamic, with no saccade, just with eye deviation within the orbit towards one position or another) upon neural responses to auditory stimuli have now been described in several cortical and subcortical structures, for cats and monkeys (Jay & Sparks, 1984, 1987; Russo & Bruce, 1994; Stricanne, Andersen & Mazzoni, 1996; Groh, Trause, Underhill, Clark & Inati, 2001; Groh, Kelly & Underhill, 2003; Werner-Reiss, Kelly, Trause, Underhill & Groh, 2003). For instance, auditory receptive fields of superior-colliculus neurons can change spatially when the eyes are directed at a different fixation location, even when the head and ears remain stationary (Jay & Sparks, 1984, 1987; Hartline, Vimal, King, Kurylo, & Northmore, 1995; Peck, Baro & Warder, 1995). In primate lateral intraparietal cortex, memory activity for sounds can be affected by the current position of the eyes in their orbits (Stricanne et al., 1996). In primate frontal eye fields, neural responses related to auditorily-guided saccades can depend on auditory target location with respect to the current direction of gaze (Russo & Bruce, 1994). More recently, some modulations of neural responses to sound location as a function of eye-position have also been described within the auditory pathway, in auditory cortex (Werner-Reiss et al., 2003) and even inferior colliculus (Groh et al., 2001, 2003; Zwiers, Versnel & Van Opstal, 2004).

In addition to this neurophysiological literature, a long tradition of psychophysical studies in humans has examined the consequences of deviated static eye position (orbital deviation, rather than eye movements *per se*) on sound localisation. While early studies addressing this issue provided some apparently conflicting or negative evidence (e.g., Ryan & Schehr, 1941; Bohlander, 1984; Weerts and Turlow, 1971; Lackner, 1973), systematic effects on perceived sound location due to eccentric, static eye-deviation have since been documented in more recent years. Lewald and colleagues in particular (e.g. Lewald and Ehrenstein, 1996a, 1996b; Lewald, 1997, 1998) have examined effects of statically deviated eye-position on auditory space perception, using various types of sounds (e.g. dichotic or free-field) and different measures of sound localisation (e.g. comparing sound position to the egocentric midline, or to a central visual reference; or pointing to sounds using a laser controlled by a central knob, or using a central swivel-pointer). In these studies, small but consistent shifts of apparent sound location were reported, on the order of ~2-3 degrees of azimuth in magnitude, when eyes were directed to one eccentric side vs. centrally. For instance, in a study in which participants were instructed to aim at the sound source using a hand-controlled swivel-pointer rotating on a central axis, participants pointed further to the right of the actual location of the sound (which unknown to the participants was always

central), when their eyes were directed in a fixed manner towards the left (Lewald, 1998). On average, the mean sound localisation error was +2.7 degrees to the right when eye position was -45 degrees to the left, and -3.5 degrees to the left when eye position was +45 degrees to the right (Lewald, 1998, page 211; negative and positive values used to indicate positions to the left or right of the body midline, respectively). Although in some cases interpretation of related findings on effects of static eye-deviation can be complicated by the possibility that, say, eye deviation might affect some reference point that is required for the requested judgement (e.g. subjective midline, or central visual reference; cf. Lewald & Ehrenstein, 2000), rather than affecting only sound perception per se, nevertheless when taken together these studies do indicate that static eye-deviation towards one particular eccentric side tends to shift perceived sound location slightly in the opposite direction, particularly when eye position deviates substantially from sound-sources located near the medial plane (e.g. Lewald and Ehrenstein, 1998; Lewald, 1998).

In contrast to this extensive research on the impact of statically deviated eye position upon sound localisation, to our knowledge relatively little behavioural research has been conducted on possible implications of dynamic changes of eye-position (i.e. eye-movements) for auditory spatial cognition, despite much discussion of the importance of re-aligning representations of visual and auditory space across eye-movements (e.g., Jay & Sparks, 1984, 1987; Groh et al., 2001; Lewald and Ehrenstein, 1998). The current relative lack of auditory studies on any eye-movement effects also contrasts with the growing literature reporting trans-saccadic effects on visual cognition (e.g. see Ross, Morrone, Goldberg & Burr, 2001; Morrone, Ross & Burr, 2005; Melcher & Morrone, 2003; Melcher, 2007), including those studies showing that directional biases can be observed when pointing to visual targets after an eye movement (e.g., Henriques & Crawford, 2000). The very few studies to our knowledge that have examined whether dynamic changes of eye-position have any distinctive impacts on auditory cognition seemed to indicate that this might not be so (Goossens and Van Opstal, 1999; Kopinska & Harris, 2003; Vliegen et al., 2004).

Van Opstal and colleagues (Goossens & Van Opstal, 1999; Vliegen et al., 2004) used double-step visuo-auditory paradigms, in which participants were instructed to make a combined eye-head movement towards an auditory target, after a previous eye-head shift towards a visual target. Regardless of whether the target sound was presented before all eye-head movements (Goossens & Van Opstal, 1999), or during the first eye-head shift towards the visual target (Vliegen et al., 2004), participants proved remarkably accurate in their sound-localising motor responses, and the intervening eye and head movements were on average fully compensated for. This result suggests that the brain is capable of constructing a stable (motor-related) representation of auditory space across eye and head movements, at least when planning and executing sound-directed spatial motor actions. Vliegen and colleagues (2004) suggest that the eyes and head are each driven by a common gaze-displacement signal (created by integrating head-centred target location with head orientation in space; i.e., world-centred coordinates) which is then decomposed in two different motor commands for the eyes and the head (in their own appropriate reference frame), by using an eye-position signal downstream from the common gaze centre (see models in Vliegen et al., 2004, p.9301; and Goossens & Van Opstal, 1997, p.558).

Using a different paradigm, Kopinska and Harris (2003) reported apparently no evidence for eye-centred coding of sound location. They asked participants to remember the location of an auditory target, and then move their eyes, or their head and eyes, or their body (beneath a stationary head), before repositioning an auditory probe to match the remembered location of the previous target. Sound localisation was modulated by head-on-body position, but no effect of eye-movements alone on sound localisation emerged. We note, however, in their

study Kopinska and Harris presented all sounds intracranially through headphones. Thus, it remains possible that an impact of eye-movements on sounds might be more pronounced for free-field auditory stimuli (as used in the present study) than for sounds perceived inside the head (as in Kopinska & Harris, 2003). This is because any re-alignment of auditory and visual maps after intervening eye movements may be more important for keeping the multisensory integrity of objects occurring in the *external* world, rather than matching artificial sounds heard intracranially to visual events in the external world (see Pavani, Husain, Ládavas & Driver, 2004 for a discussion of some neuropsychological results related to this).

Accordingly, here in the present study we investigated the possible impact of eye-movements on auditory spatial cognition, in a free-field auditory task, that did not require any sound-directed spatial actions. We assessed whether intervening eye-movements might affect performance in a perceptual short-term matching task, involving same/different comparison of the azimuth for two sounds across an intervening delay of 2.5 secs (thus analogous to some of the ‘delay’ paradigms in which possible updating of spatial representations, due to an intervening eye-movement occurring during the delay, has recently been studied for visual targets, e.g. Merriam, Genovese & Colby, 2003, 2007) . Note that in the current paradigm all auditory targets were presented several hundreds milliseconds before (or after) any intervening eye-movement took place. This was specifically designed to avoid any overlap between auditory sensory processing and actual eye-movements, thus potentially highlighting instead any possible effect of the intervening eye-movement on the remembered location of the sound. This aspect of the paradigm is somewhat similar to Kopinska and Harris (2003), albeit now using free-field sounds; but differs from several previous studies in the visual modality that examined localisation for visual targets presented peri-saccadically (for reviews of that approach, see Ross, Morrone, Goldberg & Burr, 2001).

Experiment 1

We required participants to judge whether two successive sounds, separated by an interval of 2.5 seconds and presented in free-field, originated from the same or different azimuth. While performing this task with restrained head position, participants directed their eyes to one or other of two visual fixation-points, to the far left or far right of an array of five loudspeakers (see Figure 1). On half of the trials, after presentation of the first sound (S1), the current visual fixation point briefly changed colour to instruct participants to shift their eye position to the other illuminated fixation point (on the other side of the loudspeakers array, 50 degrees away; see Figure 1b), prior to the second sound (S2) being presented. On the other half of randomly intermingled trials, the current visual fixation flickered briefly after S1, but without changing colour. This instructed participants to maintain the current fixation for now (see Figure 1a).

Since the head remained fixed (see Methods), any intervening eye-movement would not change inputs to the ears, nor the remembered location of S1 relative to the head. But it would shift (remembered) auditory locations relative to current eye position. If any eye-centric coding of auditory position contributes to the present auditory task (of comparing sound azimuth across a 2.5 second delay), then we might expect some disruption of performance when an eye movement intervenes (and thus all eye-centric positions change), even though the auditory inputs that had to be compared remain unchanged in themselves. On the other hand, if intervening eye-movements do not affect auditory spatial cognition, then no difference in performance should be found between the case where eye position remained constant (Fig 1a) and the case where it shifted substantially during the intervening delay (Fig 1b).

In addition, when considering the eye-centric position of S1 before and after a substantial intervening eye-movement (see Fig 1b), it is evident that a stimulus S1 occupying (say) a rightwards location with respect to the current line of fixation before the eye-movement, will inevitably occupy a more leftwards eye-centric position after the eyes moved from (say) left to right (Fig 1b). If eye-centric coding of auditory position can contribute to the present auditory task, as hypothesised earlier, then we should expect that subjects might then become less sensitive to changes in auditory azimuth that are in the opposite direction to the intervening eye-movement (i.e., those changes arising when S2 actually shifts towards the side that had initially been fixated, prior to the eye-movement). This is because the hypothesised internal shift in represented eye-centric location would act to oppose the actual shift in head-centric location of S2. This first possibility is illustrated schematically in Figure 2a.

An alternative prediction is however possible. If any eye position effect in the present dynamic eye-movement paradigm were to reflect just the static position of the eyes (orbital angle) during S1 or S2, then presumably it should take a similar form to the phenomena repeatedly documented by Lewald and colleagues (e.g. Lewald and Ehrenstein, 1996a, 1996b; Lewald, 1997, 1998), when actually using static eye-deviations rather than dynamic changes as here. As mentioned earlier, any effect with statically deviated eye position typically takes the form of sound localization apparently shifting in the opposite direction to the current static deviation (e.g. a sound being reported as more leftward when eye position is deviated right, or vice-versa). Extrapolating this to our situation (hence now with a possible change from leftward to rightward eye position – or vice-versa – between two successive sounds) would lead one to expect that subjects might become less sensitive to changes in auditory location that are in the same direction as the intervening eye-movement (i.e., changed arising when S2 actually shifts away from initial fixation). This second possibility, which is clearly conceptually opposite to the previous one, is illustrated schematically in Figure 2b.

As will become clear, our results accorded more with the former possibility rather than the latter. Thus our subjects actually became less sensitive to a change in auditory location when that change was in the opposite spatial direction to an intervening eye-movement (i.e., when S2 actually shifted towards the initially fixated side, on those trials with eye-movements).

Methods

Participants—Ten participants (6 women, 4 men; mean age 26 years) were recruited through advertisement. All had normal hearing on standard pure-tone audiometry (Guymark, GSI 17); reported normal or corrected-to-normal visual acuity; and were naïve as to the purpose of the experiment. Two participants were left-handed by self-report. The experiment lasted approximately 1.5 hours. Informed consent was obtained from all participants and the experiment was carried out according to the principles laid down in the Declaration of Helsinki, and as approved by the local Ethics Committee.

Apparatus and materials—Participants sat at a table in a dimly lit sound-proof room, 70 cm in front of the apparatus. Their head movements were fully restrained by an adjustable chin rest which included two lateral, adjustable stands to hold the head rigidly near the temples, and thereby keep head-direction constant. The remaining apparatus comprised 5 piezoelectric loudspeakers (0.4W, 8Ω), arranged horizontally at ear level and mounted on a semicircular plastic panel (height 30 cm, length 150 cm, radius 70 cm, distance from subject of 70 cm; see Figure 1). With respect to the participant's midsagittal plane, 2 loudspeakers were placed on the left (at minus–10 and minus–20 degrees); 2 loudspeakers were placed on the right (+10, +20 degrees); and 1 loudspeaker was placed centrally (0 degrees). Two

multicolour (green-red) LEDs were also mounted on the plastic panel, 5 cm below the level of the loudspeaker centres, at +25 and –25 degrees; these served to mark possible visual fixation locations.

Loudspeakers and LEDs were connected to a laptop computer (Dell Latitude LS) via a 32-bit high-speed digital I/O PCMCIA card (DAQCard-6533, National Instruments) and a custom electronic interface. Timing of stimuli and responses was controlled by the laptop computer, via the I/O interfaces, using custom software developed with MATLAB 6 and Cogent 2000 (<http://www.fil.ion.ucl.ac.uk>). Eye-position was monitored throughout each trial using a remote eye-tracker (ASL Model 504; sampling and output rate 60Hz, resolution 0.25 degree of visual angle) connected to the laptop computer via a control unit (ASL Model 5000). A second laptop computer (NEC Versa S/33) operated the eye tracker using the E5000 EYEPOS software package. This was also interfaced with the custom software controlling the stimuli, allowing on-line eye-movement data recording and monitoring.

Procedure—At the beginning of each experimental block, both LEDs were illuminated green and participants fixated one or other of the two lights (the one that flashed intermittently at 1Hz for 2 seconds) for the start of the upcoming block. After a further 500 ms (i.e., 2500 ms from when they acquired visual fixation) the first auditory stimulus (S1, comprising a 250 ms burst of white noise presented at approximately 60dB as measured from the participant's head) was delivered through one of the three speakers located at –10, 0 or +10 degrees. 1000 ms after the offset of S1, fixation was either briefly extinguished for 100 ms (without change in colour), or temporarily turned red for 100 ms. This red flash instructed participants to shift their gaze to the other illuminated fixation point (on the other side, 50 degrees away); whereas if the light remained green this indicated that the initial fixation had to be maintained (see example eye data at bottom of Fig 1a, confirming adherence to this instruction). After a further 1400 ms (thus 2500 ms after S1 offset), the second auditory stimulus (S2, also a 250 ms burst of white noise, at approximately 60dB) was presented for 250 ms. This could either be delivered from the same speaker as S1 (thus producing a ‘same’ trial), or from one of the speakers located 10 degrees to one or other side of S1's original position (thus producing a ‘different’ trial). Note that the timing within each trial was such that auditory targets were always presented while eye position was static (as confirmed with eye-tracking), since 2.5 secs intervened between S1 and S2, which was always more than sufficient to allow any intervening eye-movement to be completed (see example eye-data at bottom of Figure 1b, that illustrate clearly the temporal separation between the two successive auditory targets and the intervening eye-movement). Note also that when either of the sounds were presented visual fixation was not flickering, thus precluding visual capture of sound towards the flickering location (i.e., avoiding any possible ‘ventriloquist’ effect, which depends on temporal synchrony between visual and auditory stimuli). After S2 presentation, the participant made a speeded verbal response about auditory location, by saying ‘same’ or ‘different’. Participants' discrimination responses were typed into the computer by the experimenter; audiotapes of the vocal response were also digitally recorded for off-line vocal RT analysis (see Footnote). If no discrimination response was made within 3000 ms, the trial was terminated; otherwise the response ended that trial and started the next one.

Before the experiment, participants were informed that two sounds would be presented sequentially on each trial, and that their task was to decide whether this pair of successive sounds came from the same or different locations (only azimuth was varied). They were also instructed to obey the colour signals presented at visual fixation and, if an eye-movement was required, to acquire the new fixation position (far on the other side) and then maintain that new fixation location until further eye-movement instructions were given there. Participants were briefly trained separately in the sound localisation task, and then in the

eye-movement task (10 practice trials for each task). Ten additional practice trials were then also carried out on the two tasks when interleaved. These practice trials were not analysed. Practice was followed by 4 experimental blocks of 72 trials each, for a total of 288 trials. These consisted of 96 'same trials' (S1 and S2 presented from the same speaker) and 192 'different trials' (S1 and S2 presented from different speakers). S1 and S2 position were unpredictable on every trial and the sequence of 'same' or 'different' trials was randomised between participants. For each participant, initial fixation side alternated between blocks; half of the participants started with right fixation and the other half with left fixation. Fixation was stationary in half of the trials and shifted between presentation of S1 and S2 in the other half, with these two types of trial randomly intermingled.

Data analysis—As a function of S1 position, we examined participants' ability to detect any changes in auditory location/azimuth, both for eyes-static trials, and separately for trials when an eye-movement intervened (although note that eyes were always fixed at one or other location during the sounds in the latter condition also, moving between the two fixation locations only in the intervening delay between the sounds, see Figure 1b). Each S1 position was recoded as inner, middle or outer with respect to initial fixation (i.e., -10 , 0 and $+10$ degrees constituting respectively the inner, middle and outer S1 locations when eyes were directed leftwards at -25 degrees; whereas $+10$, 0 and -10 degrees constituted respectively the inner, middle and outer S1 locations when eyes were directed rightwards, at $+25$ degrees). In addition, because previous work has shown some systematic directional shifts of reported sound position as a function of static eye-direction (e.g., see Lewald and Ehrenstein, 1996a, 1996b; Lewald, 1997, 1998), typically in the direction opposite to statically deviated fixation (see introduction), we also expressed any sound-position change for different-location trials with respect to initial fixation. Specifically, we distinguished between different-location trials in which S2 appeared at a location more towards initial fixation than S1 itself (i.e., S2 shifts towards initial fixation), versus different-location trials in which S2 appeared at a position further away from initial fixation than S1 (i.e., S2 shift away from initial fixation).

Our main dependent measures were accuracy (percent correct) and sensitivity (d'). Sensitivity was computed using signal detection procedures modified for same-different designs (Macmillan & Creelman, 1991). Sensitivity was calculated based on the hit rate for detecting a sound location change (i.e., 'different' response produced in a true different-location trial), separately for each specific S1 location; and the false alarm rate for the corresponding S1 location (i.e., 'different' response produced when the two sounds were in fact presented from the same position).

Greenhouse-Geisser correction was applied to the Analysis of Variance (ANOVA) when appropriate. T-tests were used for planned comparisons, and Newman-Keuls tests were used for post-hoc contrasts.

Results

Across all participants, 8% of trials were removed and not analysed because of failure to follow eye-movement instructions or due to blink artefacts. Instructed eye-movements began on average 532 ms after onset of the instruction (red flicker) at fixation. The new fixation point was stably acquired on average 362 ms later. All eye-movements were completed well before S2 onset (which was 2.5 secs after S1 offset). Thus, the timing of the trial proved effective for allowing substantial eye-movements to be completed in the intervening delay after offset of S1 but before onset of S2 (see also Fig 1b for examples of actual eye-data in relation to the timing of stimulus events). Approximately half of the eye-movements (48%) were completed with a single identifiable saccade, whereas the remaining eye-movements

were completed with 2 (41%), 3 (10%) or even 4 distinguishable saccades (1%). This is expected given the eccentricity of the far-left and far-right visual locations, compatible with the accepted notion that long range eye-movements often involve multiple saccades. However, the important point to note for present purposes is that the number of saccades required to complete the eye-movement (i.e., the percentages of trials with 1, 2, 3, and 4) did not differ as a function of the relative position of S1 and S2 (i.e., was statistically equivalent for same-sound trials, different trials in which S2 shifted towards initial fixation, or different trials in which S2 shifted away from initial fixation).

Figure 3a shows mean accuracy (percent correct), separately for same and different trials, as a function of the presence or absence of an intervening eye-movement. For same-location trials, participants were less accurate when an intervening eye-movement occurred (mean = 84%) than when the eyes remained static (mean = 99%; $t(9) = 2.5$, $p < 0.03$). In addition, worse performance during eye-movements (mean = 41%) than for eyes-static trials (mean = 77%; $t(9) = 6.2$, $p < 0.0001$) emerged on different-locations trials when S2 shifted towards initial fixation. By contrast, no reduction of accuracy for eye-movement trials emerged when S2 appeared further away from initial fixation with respect to S1; in fact, there was now a marginal trend for slightly better accuracy on eye-movement (mean = 86%) than eyes-static trials (mean = 78%; $t(9) = 1.85$, $p = 0.1$). A two-way Analysis of Variance (ANOVA) with eye-movement (present or absent) and relative S1-S2 position (same; or different with sound shift towards initial fixation; or different with sound shift away from initial fixation) as factors, confirmed an interaction between these factors ($F(2,18) = 15.6$, $p < 0.0001$, $\epsilon = 0.84$; see Figure 3a).

Although our task required a non-speeded response, for completeness we also analysed mean reaction times (RTs) for correct trials. RTs were significantly longer in the conditions that also led to worse accuracy, ruling our speed/accuracy tradeoffs as an explanation for these observed effects (see Footnote ¹).

To further examine the results, sensitivity (d') was computed (see Table 1). An ANOVA on the d' data had the within-participant factors of eye-movement (present or absent), direction of auditory change on different-trials (S2 shifting towards or away from initial fixation) and S1 location (inner, middle or outer with respect to initial fixation). This confirmed that a reduction in sensitivity on eye-movement trials did emerge specifically when S2 shifted towards initial fixation with respect to S1 (eye-movement trials for this situation had mean $d' = 1.83$; eyes static trials had mean $d' = 3.12$; $p < 0.0001$ on post-hoc test); but not when S2 shifted away from initial fixation (eye-movement trials for this situation had mean $d' = 2.83$; eyes static trials had mean $d' = 3.13$; $p = 0.2$). This resulted in a two-way interaction between eye-movement and direction of auditory change ($F(1,9) = 14.3$, $p < 0.004$; see Figure 3b).

The d' analysis also revealed that this directionally-specific reduction of sensitivity during eye-movement trials emerged when S1 appeared at middle and outer locations (with respect to initial fixation; $p < 0.0001$ for both comparisons between 'towards' vs. 'away' trials at these S1 locations), but was absent when S1 appeared at the inner location ($p = 0.1$; see Table 1). This resulted in a significant 3-way interaction between eye-movement, direction

¹Participants responded more slowly for eye-movement (mean = 661 ms) than eyes static trials (mean = 533 ms; $t(9) = 4.7$, $p < 0.001$) when S1 and S2 appeared at the same location. Similarly, longer RTs emerged for eye-movement (mean = 872 ms) than eyes static trials (mean = 590 ms; $t(9) = 6.1$, $p < 0.0002$) on different-locations trials that involved an actual shift of the sound towards initial fixation. By contrast, no difference between the two eye position conditions emerged on different-location trials when S2 appeared further away from initial fixation than S1 (eye-movement trials mean = 636 ms; fixed-gaze trials mean = 610 ms; $t(9) = 0.9$, $p = 0.4$). An ANOVA, similar to the one applied to the accuracy data with eye-movement and relative S1-S2 position as factors, confirmed a two-way interaction ($F(2,18) = 9.6$, $p < 0.002$, $\epsilon = 0.92$), in accord with the comparisons of means.

of auditory change, and S1 location ($F(2,18) = 7.7$, $p < 0.007$, $\epsilon = 0.81$). In addition there was a main effect of eye-movements ($F(1,9) = 28.2$, $p < 0.0001$), a main effect of direction of auditory change ($F(1,9) = 24.1$, $p < 0.001$) and an interaction between eye-movement and S1 position ($F(2,18) = 9.9$, $p < 0.006$, $\epsilon = 0.67$), but these terms were all subsidiary to the higher-order interactions.

Discussion

The results of Experiment 1 clearly reveal that when participants make a same/different discrimination of two successive sounds (separated by 2.5 secs), a substantial intervening shift of eye position can lead to considerably worse performance (as measured by percent correct and d') with respect to when stable fixation is maintained. But importantly this disruption of performance was highly specific, rather than just representing some general 'dual-task' decrement. In particular, the impaired performance due to an intervening eye-movement was strictly dependent on the spatial relationship between the two successive sounds and the direction of the intervening eye-movement.

When S1 and S2 appeared at different locations, a decrement of discrimination ability for the eye-movement condition emerged only when S2 moved further towards initial fixation (i.e., for an actual auditory shift in the opposite direction to the intervening eye-movement), but not when S2 moved away from initial fixation with respect to S1 (i.e., an actual auditory shift in the same direction as the intervening eye-movement).

The directional selectivity of these results means that the decrement cannot be attributed merely to some overall 'dual-task demand' when some eye-movement intervened between the successive sounds. Instead, we suggest that it may reflect a directional error in (remembered) representation of auditory location caused by the intervening eye-movement (see Fig 2a). In particular, we hypothesize that a representation of the first sound (S1) in spatial working memory may shift somewhat in the opposite direction to the eye-movement (i.e. becoming represented as more leftward than it was initially, following a left-to-right eye position shift; or as more rightward, following a right-to-left eye position shift). This is compatible with the existence of some eye-centric updated representation of S1, as anticipated in the Introduction, and the hypothesis clearly accords with the directional aspect of our results. We consider why this might arise in more detail in our General Discussion. But first, we present a follow-up to Experiment 1, which repeated the same design while removing possible visual cues to the location of sound sources.

Other than the eye-movement, our task logically required only an auditory comparison of the two sounds across the intervening delay, and then a verbal response. However the loudspeakers were all fully visible in Experiment 1. This may have favoured some eye-centric coding of sound locations that might otherwise not have arisen. If so, then simply removing all visual cues as to sound source locations should completely eliminate all the effects of eye-movements on the auditory task. We tested this directly in Experiment 2.

Experiment 2

In Experiment 2, a large polyester curtain (an acoustically transparent close weave cloth, specifically designed for mounting on loudspeaker grilles when cut smaller than the complete sheet used here; Model: KS50E, Maplin, UK) was placed singly in front of the entire apparatus to completely prevent vision of all the loudspeakers, throughout the entire experiment. Only the two possible fixation lights were visible when illuminated, shining through the curtain (note that the light emitted by these LEDs was too focal, weak and distant from the loudspeakers to illuminate any of those speakers unintentionally). In all other respects, the experimental procedure remained unchanged. If the clear effect of eye-

movements on the auditory task, as found in Experiment 1, requires full vision of the loudspeakers, it should be eliminated in Experiment 2. By contrast, if it reflects eye-centric influences on strictly auditory spatial cognition, then we should find some similar results even in the total absence of any vision of the loudspeakers.

Methods

Participants—Ten new participants (6 women, 4 men; mean age 21 years) were recruited as before. All had normal hearing on standard pure-tone audiometry (Guymark, GSI 17), normal or corrected-to-normal vision by self-report, and were naïve as to the purpose of the experiment. Two participants were left-handed by self-report. Informed consent was obtained from all participants.

Apparatus, material and procedure—These were identical to Experiment 1 with the following exception. A large (2×1.5 m) acoustically-transparent black-felt cloth was now stretched between the walls of the sound-proof room, and hung from the ceiling, as a curtain between the participant and the apparatus. This completely prevented vision of the apparatus and the speakers. Only the two possible fixation lights were visible when illuminated, shining through the cloth. Note that the black walls of the window-less sound-proof cabin also contributed to creating a uniform black visual scene (with the sole exception of the faint point of light from the LEDs).

Results

Across all participants 7% of trials were removed from analysis because of failure to follow eye-position instructions, or due to blink artefacts. Instructed eye-movements occurred on average 587 ms after onset of the instruction at current fixation, and a new fixation was acquired on average 325 ms later. All eye-movements were completed before S2 onset. Once again, eye-movements never overlapped with auditory presentation of S1 or S2. As in Experiment 1, approximately half of the eye-movements (60%) were completed with a single identifiable saccade, whereas the remaining eye-movements were completed with 2 (34%), 3 (5%) or even 4 distinguishable saccades (1%). But the more important point is that, once again, the number of saccades required to complete the eye-movement (i.e., the percentages with 1, 2, 3, and 4) did not differ as a function of the relative position of S1 and S2 (i.e., was statistically equivalent for same trials, different trials in which S2 shifted towards initial fixation, or different trials in which S2 shifted away from initial fixation).

Mean discrimination accuracy is shown in Figure 4a as a function of the presence or absence of intervening eye-movements and the relative position of S1 and S2. For same trials, discrimination accuracy tended to be worse for eye-movement (mean = 92%) than eyes static conditions (mean = 96%; $t(9) = 1.92$, $p = 0.08$). Importantly, accuracy was significantly worse for eye-movement (mean = 68%) than eyes-static trials (mean = 83%; $t(9) = 3.18$, $p < 0.01$) when S2 appeared further towards initial fixation with respect to S1 (as also in Experiment 1).

Interestingly, for different-trials with an auditory change away from initial fixation, discrimination accuracy actually became higher for eye-movement (mean = 84%) than eyes static trials (mean = 78%; $t(9) = 3.17$, $p < 0.01$), analogously to the marginal trend for this in Experiment 1. An ANOVA with eye-movement (present or absent) and relative S1-S2 position (same; or different with an auditory change towards initial fixation; or different with an auditory change away from initial fixation) as factors confirmed a two-way interaction once again ($F(2,18) = 11.4$, $p < 0.002$, $\eta^2 = 0.75$; see Figure 4a). As for Experiment 1, the RT pattern rules out speed/accuracy trade-offs as an explanation for the significant differences in accuracy reported above (see Footnote 2).

Mean sensitivity (d') measures are reported in Table 2. An ANOVA on the d' data had the factors of eye-movement (present or absent), direction of auditory change (S2 appearing towards or away with respect to initial fixation) and S1 location (inner, middle or outer with respect to initial fixation) as within-participants factors. This once again confirmed a selective reduction of sensitivity when a eye-movement intervened between the two sounds and S2 moved further towards initial fixation with respect to S1 (eye-movement trials in this situation has a mean $d' = 2.65$; eyes static trials mean $d' = 3.19$; $p < 0.003$ on post-hoc test). By contrast, no effect of eye-movements on d' emerged when S2 moved away from initial fixation (eye-movement trials in this situation had a mean $d' = 3.03$; eyes-static trials mean $d' = 3.02$; $p = 0.9$). This resulted in a two-way interaction between eye-movement and direction of auditory change ($F(1,9) = 15.3$, $p < 0.004$; see Figure 3b).

In addition there was a significant interaction between direction of auditory change and S1 position ($F(2,18) = 13.9$, $p < 0.003$, $\epsilon = 0.59$), caused by reduced discrimination sensitivity for inner S1 locations when S2 appeared further toward initial fixation, but for outer S1 locations when S2 appeared further away from initial fixation (see Table 2). While this specific result was not expected and so will not be discussed further, it is important to notice that this particular interaction did not involve the eye-movement factor (the three-way interaction was not significant, $F(2,18) = 1.6$, $p = 0.2$), so is tangential to our main concerns. The only other significant terms in the ANOVA were the main effects of eye-movement ($F(1,9) = 8.2$, $p < 0.02$) and of S1 position ($F(2,18) = 5.9$, $p < 0.02$, $\epsilon = 0.69$), but these are subsidiary to higher order interactions.

Discussion

Experiment 2 was performed to examine the effects of removing any visual information about the location of the sound-sources (i.e. vision of the loudspeakers, due to the occluding curtain). In this successive same/different auditory task, that in principle could be performed solely by relying on auditory information entering the ears, intervening eye-movements (during the delay between the two successive sounds) nevertheless significantly affected discrimination of sound position. Rather similarly to Experiment 1, this effect depended upon the relationship between the relative position of the two successive sounds and the direction of the intervening eye-movement. Discrimination sensitivity was significantly decreased for an actual shift of S2 towards initial fixation with respect to the initial sound (i.e., opposite the direction to the intervening eye movement). Changes of S2 position away from initial fixation with respect to the initial sound (i.e., in the same direction as the intervening eye-movement) resulted in comparable discrimination sensitivity.

Although directionally-specific impacts of eye-movement remained evident even when the loudspeakers could not be seen (Experiment 2), a visual comparison of the results against those for Experiment 1 (compare Figures 3 and 4) suggests that intervening eye-movements had a somewhat bigger detrimental effect on performance when loudspeakers were visible rather than invisible. To assess this statistically, we calculated the difference in performance between eye-movement and fixed-gaze trials (i.e., the cost of intervening eye-movements for performance) on sensitivity (d'), and entered this in a mixed ANOVA on different trials, with experiment (speaker visible or invisible) as a between-participants factor, and direction

²Participants responded more slowly for eye-movement (mean = 772 ms) than eyes static trials (mean = 712 ms; $t(9) = 2.7$, $p < 0.02$) when S1 and S2 appeared at the same location. The trend for a difference in RTs between eye-movement and eyes static trials on different-location trials with an auditory change towards initial fixation did not reach full significance (mean = 821 ms and 770 ms, respectively; $t(9) = 1.9$, $p = 0.1$), and likewise for different-location trials with an auditory change away from initial fixation (mean = 782 ms and 765 ms, respectively; $t(9) = 0.8$, $p = 0.4$). But a two-way ANOVA, similar to the one used for accuracy data, did reveal a main effect of eye-movement ($F(1,9) = 6.1$, $p < 0.04$) that did not interact with relative S1-S2 position ($F(2,18) = 1.2$, $p = 0.3$).

of auditory change (S2 changing towards or away with respect to initial fixation) as a within-participants factor.

This revealed a main effect of experiment ($F(1,18) = 36.2, p < 0.008$) caused by larger eye-movement costs overall when speakers were visible (Exp.1, mean cost on $d' = 0.80$) than invisible (Exp.2, mean cost on $d' = 0.27$). But importantly there was no interaction between experiment and direction of auditory change ($F(1,18) = 2.1, p = 0.2$), indicating that the despite the somewhat smaller cost of intervening eye-movements overall when speakers were invisible, the most critical directionally-selective aspect of this cost remained comparable across the two experiments.

General Discussion

To our knowledge, the present findings provide the first behavioural evidence for clear and highly specific effects from intervening eye-movements during a task that required an auditory same/different perceptual comparison (across a delay) rather than a spatial motor response towards a sound (cf. Goossens & Van Opstal, 1999; Vliegen et al., 2004). Discrimination of the relative location (in azimuth) of two successive sounds separated by a delay of 2.5 seconds was worse when participants made substantial eye-movements during the delay than when they maintained stable fixation. Importantly, the reduced sensitivity to changes in sound position during eye-movement trials emerged in a highly selective manner, being most pronounced when the actual location of the second sound had shifted towards the original point of fixation (i.e., in the opposite direction to the intervening eye-movement; see Figs 3c and 4c). This finding implies that the eye-movement introduced a directional error in spatial representations of sound location.

Although our paradigm does not reveal which of the two auditory stimuli (S1, S2, or both) was most affected by this directional error, we suggest that a parsimonious account may be to link our critical direction result with some gaze-centric recoding/updating of the remembered initial sound, i.e., S1 (see also Jay & Sparks, 1984, 1987; Russo & Bruce, 1994; Stricanne et al., 1996; Groh et al., 2001; Werner-Reiss et al., 2001; Zwiers et al., 2004, for neurophysiological evidence). We hypothesize that the spatial location of S1 may be updated in memory when its gaze-centric coordinates are modified as a consequence of the eye-movement (and therefore represented as more 'leftward', eye-centrally, following a rightward eye-movement, and vice-versa). This proposal accords with the directional nature of the new effect we have uncovered.

In any case, the highly specific (directional) nature of the disruption caused by an intervening eye-movement shows that the impaired performance cannot merely be attributed to some overall 'dual-task' cost when shifting eye position as well as making auditory judgements, as only certain auditory situations were impaired, not all. Similarly, it indicates that participants were not solving the auditory task through mere verbalisation of the active loudspeakers in each trial (e.g., 'speaker 1' then 'speaker 2'), since this strategy would have been unaffected by the direction of the intervening eye-movement.

Notably, although the costs of intervening eye-movements were larger overall when sound sources were visible (Exp. 1), the directional nature of the effect was preserved even when vision of the sound-sources and apparatus was completely prevented (Exp. 2). This underlines that effects of eye-movements on auditory spatial cognition are not merely due to visual input.

Three previous studies with some relations to the present one did not reveal any distinctive impact of dynamic changes of eye-position on auditory cognition (Goossens and Van Opstal, 1999; Kopinska & Harris, 2003; Vliegen et al., 2004). They concluded that a stable

representation of the sound is created based on head-centred target location and head-orientation in space (Kopinska & Harris, 2003; Vliegen et al., 2004). We suggest that at least two factors could be responsible for the difference between our clear new finding and those previous results. In the studies by Goossens & Van Opstal (1999) and Vliegen et al. (2004), participants were required to make a spatial motor response, directing eye-head movement to the auditory targets. By contrast, in the current paradigm, a perceptual same/different judgement was required (i.e., judge whether the two consecutive sounds occurred from same or different locations, across the delay).

As suggested by Vliegen et al. (2004, their p. 9300), it is possible that “the mechanisms underlying action (rapid orienting) and perception (voluntary judgements) use different computational strategies, weightings and neural pathways to update the frames of reference”. Interestingly, Vliegen et al. also suggest that target updating for goal-directed actions towards sensory stimuli may rely upon continuous updating of instantaneous changes in eye and head orientation (e.g., Goossens & Van Opstal, 1999; Vliegen et al., 2004). By contrast, trans-saccadic mechanisms serving spatial perception of the sensory scene may also involve some predictive remapping of upcoming motor commands for the eyes and/or head (e.g., see Duhamel, Colby & Goldberg, 1992; Umeno & Goldberg, 1997).

In the study by Kopinska and Harris (2003), participants were asked instead to adjust an auditory probe to match the location of a previously presented target sound, after an intervening movement of the eyes, head and eyes, or body (beneath a stationary head) had occurred between target sound and localisation with auditory probe. Thus, it required a perceptual rather than motor response, somewhat similar in this respect to the current study. However, unlike the current study, in which all sound stimuli were delivered free-field, auditory targets in Kopinska & Harris (2003) were always presented through headphones and perceived intracranially. In other words, sounds in their study were lateralised using only interaural level difference (ILD) as the sole spatial auditory cue (i.e., there was no attempt to create a virtual auditory space, using individual Head-Related Transfer Functions). We speculate that eye-centric recoding of sounds may particularly apply for sounds occurring in extrapersonal space, for which the need to re-alignments auditory and visual space across postural changes may be more pronounced, than for artificial sounds perceived intracranially instead. In the neuropsychological literature on spatial neglect in brain-damaged patients, it has also been suggested that visual and auditory spatial cognition may be more closely tied for extrapersonal space, than for sounds perceived intracranially (e.g. see Pavani, Husain, Ldavs & Driver, 2004).

Because our paradigm involved maintenance of eccentric eye position, directed to one or other side of the apparatus (see Fig 1), in addition to the eye-movements moving the eye from one such eccentric fixation location to the other, any potential role of static eye deviation in the orbits, upon the observed directional effect also needs to be considered. But as anticipated in our Introduction, repeated findings that statically maintained eccentric eye position can influence auditory spatial cognition have typically shown sound localisation errors in the opposite direction to the statically deviated gaze (e.g. see Lewald and Ehrenstein, 1996a, 1996b; Lewald, 1997, 1998). As mentioned in our Introduction, Fig 2b presents a schematic depicting how any such influence from directions of static fixation (rather than from intervening eye-movements) would be expected to influence performance in our paradigm, as shown for a case where the actual location of S2 is further away from initial fixation with respect to S1. As can be seen from Figure 2b, the usual influence of statically deviated gaze should be expected to produce difficult S1-S2 discrimination for actual S2 shifts which are opposite to those we found to be disrupted on the eye-movement trials (namely, we observed harder discrimination for trials in which the actual position of S2 shifted towards initial fixation with respect to S1). This is not to say that static deviations

of gaze cannot influence auditory spatial localization, as other studies clearly show that they can (e.g. see Lewald and Ehrenstein, 1996a, 1996b; Lewald, 1997, 1998). But it does imply that the present highly specific eye-movement effects cannot be reduced to such prior findings on static gaze deviations (see Fig 2 legend). It would be interesting to vary parametrically both static eye-in-orbit eccentricity, and orthogonally eye-movement amplitudes, in future work with modifications of the new paradigm we have introduced, in order to assess the relative contribution of these two non-auditory influences on localisation of sounds (see Lewald & Ehrenstein, 1998b for an example of parametric variations of static eye-position eccentricity).

Although the head did not shift in our study, due to the head-restraint used as apparatus (see methods), we may need to consider also whether the substantial eye-movement could trigger internal “intended” (but not executed) head rotation plans, presumably in the same direction as the eye-movement, even when no overt head-movement took place, which might then produce some changes in the remembered head-centric location of sounds (Zwiers et al., 2004). Some tonic coupling between the horizontal component of eye position and dorsal neck muscle activity has been demonstrated in cats (Vidal et al., 1982, 1983), monkeys (Lestienne et al., 1984) and humans (André-Deshays et al., 1991), even under head-restrained conditions. Sound localisation errors produced by head-on-body signals have typically been observed in the direction opposite the apparent head-displacement (e.g., Lackner, 1973; Lewald & Ehrenstein, 1998a; Lewald et al., 1998, 2000; Kopinska and Harris, 2003). In addition, Lewald and colleagues (1998) have previously shown that such errors in sound localisation can also emerge with restrained head position (as here), when transcutaneous vibration is applied to the posterior neck muscles to induce apparent lengthening of the neck muscles and the perception of head-rotation towards the side contralateral to the neck vibration.

However, two lines of argument may challenge a purely head-centric interpretation of our findings. First, even if some internal representation of a potential head-turn is induced by the substantial eye-movements used here with a fixed head, it should be noted that the eye-movement would still provide the original cause for the effects on auditory spatial cognition that we observed (even if any internal head-centric circuits do subsequently become involved when the eye-movement is executed). Second, a recent purely visual study (Melcher, 2007) suggests that when an eye-movement is planned, a visual stimulus flashed in the intermediate location between initial fixation and the saccadic target is also mislocalised. When reporting whether the flashed visual stimulus was nearer to the initial fixation or the saccadic target, participants made small (0.91 degrees on average) but consistent displacement of the visual localization judgements towards pre-saccadic fixation (i.e. in the opposite direction to the eye-movement, somewhat analogous to our auditory findings). It may be most parsimonious to explain both sets of results (i.e. for vision as in Melcher, 2007; and for audition, as shown here) in terms of potential gaze-centric updating (see Fig 2b) arising due to the eye-movement, although further work is required to compare visual versions of the paradigm introduced here with auditory stimuli.

In conclusion, our results demonstrate for the first time an effect of intervening eye-movement on same/different sound localization (azimuth) judgements, in an auditory task that did not require a spatial motor response to the free-field sounds. We suggest that the auditory location held in memory while the eye-movement was executed may be ‘remapped’ eye-centrally, thus being remembered as having been presented from further to the left when a rightward eye-movement follows it, or further to the right after a leftward eye-movement. Eye-movements can thus contribute to auditory spatial cognition, even for (and perhaps especially for) judgements that do not require a spatial motor response. These results go beyond prior demonstrations that statically deviated eye position can influence

auditory spatial cognition, to show that dynamic changes in eye-position can also affect internal representation of auditory location.

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Figure 1.

Cartoon of the experimental paradigm shown at top of each panel, as viewed from behind the subject's head, together with plots of mean eye-trace recordings for each subject in Experiment 1 and 2 shown below in each panel. Cartoon and eye-data are shown separately for: (a) eyes static trials; and (b) eye-movement trials. Gray bars in the plot indicate presentation of the auditory stimuli (lasting 250 ms each), while the narrower green and red bars indicate presentation of the colour-coded instruction at current fixation (green for maintaining or red for changing fixation with a eye-movement, respectively; each lasting 100 ms). Width of the bars thus represents the duration of the corresponding event. Black eye-traces refer to trials with initial fixation 25 degrees to the left, grey eye-traces refer to trials with initial fixation 25 degrees to the right. Note the maintenance of deviated fixation in the eyes static trials (a); and the substantial eye-movements that were always executed after the first sound and prior to the second sound on eye-movement trials (b).

Figure 2.

Schematic representation of two types of possible influence from eye position (dynamic vs. static) upon internal representations of auditory location, see main text for discussion. The subject's head is shown schematically from behind, with potential sound-sources in front of the subject indicated here with vertical dashed lines. In this example, the subject's eyes are directed far-left at the start of the trial, then shift rightward (see arrow), to result in a new direction of static fixation on the far-right (as in Figure 1 also). The actual location of a possible first sound (S1) is shown here as a solid red circle. Its possible apparent location (on one or other hypothetical account) is then shown as a more faint red circle. The actual location of a possible second sound (S2) is shown as a solid blue circle, and its possible

apparent location (on one or other hypothetical account) as a faint blue circle. In (a), the prediction from possible eye-centric updating of S1 location after a eye-movement intervening between S1 and S2 is illustrated (see also main text for fuller explanation). Here an actual S1 location is represented as further to the left than it actually was following an intervening eye-movement to the far-right (and the reverse would apply for the opposite eye-movement, i.e. S1 would become represented as more rightward than it actually was if eye position shifted to its right, due to eye-centric updating). In (b), the expectation from prior work on purely static eye-deviations is illustrated schematically. When eye position is deviated statically to the left, S1 is expected to be perceived as slightly further to the right than it actually is; and vice versa for S2 with eye position to its right. Note that this leads to an opposite prediction than the eye-centric remapping idea for the present paradigm, namely that harder discrimination for S1-S2 pairings should emerge when S2 shifts further away from initial fixation (rather than towards initial fixation as in panel a). Our observed results were more in accord with the prediction illustrated in (a).

Figure 3. (a) Percent correct and (b) sensitivity, as a function of relative position of S1 and S2, separately for eyes static and eye-movement trials in Experiment 1 (loudspeakers visible). Brackets (or asterisks) indicate significant differences between eyes static and eye-movement trials ($p < 0.05$ or better on paired t-tests). Bars indicate standard errors.

Figure 4. (a) Percent correct and (b) sensitivity, as a function of relative position of S1 and S2, separately for eyes static and eye-movement trials in Experiment 2 (loudspeakers occluded). Brackets (or asterisks) indicate significant differences between eyes static and eye-movement trials ($p < 0.05$ or better on paired t-tests). Bars indicate standard errors.

Table 1

Sensitivity (d') for 'different' trials in Experiment 1, as a function of eye-movement, S1 and S2 position

		S2 position with respect to S1	
		Towards initial fixation	Away from initial fixation
Eyes-static trials			
	Inner S1 position	2.45	3.31
	Middle S1 position	3.52	3.37
	Outer S1 position	3.40	2.71
	Mean	3.12	3.13
Eye-movement trials			
	Inner S1 position	2.13	2.94
	Middle S1 position	1.62	3.04
	Outer S1 position	1.74	2.51
	Mean	1.83	2.83

Both S1 and S2 position are expressed with respect to initial fixation; see manuscript for details

Table 2

Sensitivity (d') for 'Different' trials in Experiment 2, as a function of eye-movement, S1 and S2 position

		S2 position with respect to S1	
		Towards initial fixation	Away from initial fixation
Eyes-static trials			
	Inner S1 position	2.76	3.30
	Middle S1 position	3.34	3.45
	Outer S1 position	3.48	2.30
	Mean	3.19	3.02
Eye-movement trials			
	Inner S1 position	2.27	3.39
	Middle S1 position	2.86	3.27
	Outer S1 position	2.82	2.43
	Mean	2.65	3.03

Both S1 and S2 position are expressed with respect to initial fixation; see manuscript for details