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Effects of attention and unilateral neglect on auditory stream segregation

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Abstract

Two pairs of experiments studied the effects of attention and of unilateral neglect on auditory streaming. The first pair showed that the build-up of auditory streaming in normal subjects is greatly reduced or absent when they attend to a competing task in the contralateral ear. It was concluded that the effective build-up of streaming depends on attention. The second pair showed that patients with an attentional deficit towards the left side of space (“unilateral neglect”) show less stream segregation of tone sequences presented to their left than to their right ear. Streaming in their right ears was similar to that for stimuli presented to either ear of healthy and of brain-damaged controls, who showed no across-ear asymmetry. This result is consistent with an effect of attention on streaming, constrains the neural sites involved, and reveals a qualitative difference between the perception of left- and right- sided sounds by neglect patients.

Effects of attention and unilateral neglect on auditory stream segregation

Auditory streaming is an example of the “grouping” or “binding” processes that have been extensively studied both in the auditory (e.g. Bregman, 1990; Darwin & Carlyon, 1995) and visual (e.g. Treisman & Gormican, 1988) domains. It is well-illustrated by the stimulus shown in Fig. 1 (van Noorden, 1975), in which a pair of tones with frequencies A and B is presented in the sequence “ABA-ABA-ABA”. When the repetition rate of the sequence is slow, or when the frequencies A and B are close, listeners can hear a galloping rhythm corresponding to the repeating triplets (Fig. 1a). However, at faster rates and wider separations, the A and B tones split into two separate streams (Fig. 1b), and the galloping rhythm is lost (Anstis & Saida, 1985; van Noorden, 1975). Additionally, the tendency for this stream segregation to occur builds up over several seconds, so that listeners may hear the gallop at the beginning but not at the end of a long sequence.

A question which has interested both auditory and visual researchers is the stage of perceptual processing at which grouping mechanisms occur. In particular, the extent to which grouping and streaming depend on attention has attracted considerable interest (Anstis & Saida, 1985; Bregman, 1990; Joseph, Chun, & Nakayama, 1997; Mack, Tang, Tuma, & Kahn, 1992; Moore & Egeth, 1997; Rock, Linnett, & Grant, 1992). In the case of audition, Bregman (1990) has distinguished between primitive mechanisms, which are largely data-driven and do not require attention, and schema-based mechanisms which are top-down and involve attentional processes. He has argued that the stream segregation of simple tone sequences, such as that shown in Fig. 1, does not always require attention. In support of this

viewpoint, he cites a study by Bregman and Rudnický (1975) in which listeners were required to compare the order of two tones, A and B, between two observation intervals (Fig. 2a). Listeners performed this task very well, but performance dropped markedly when two additional tones of a nearby frequency were added before and after the tone pair in the second interval (so that the sequence was “XABX”; Fig. 2b). Bregman and Rudnický found that adding a sequence of tones with a frequency close to X (“CCCCXABXCCCC”; Fig. 2c) improved performance, and attributed this to the “C” tones pulling the interfering “X” tones into a separate auditory stream from the target tones. He concluded that, because listeners were not required to pay attention to the C tones, the stream segregation must have occurred in the absence of attention. However, it seems likely that listeners were in fact attending to the C tones, as they were the only sounds present at the time, and there was no other task competing for attention. This is very obvious when one listens to the stimuli (Bregman & Ahad, 1995, track 16). In our first two experiments we manipulate attention more rigorously by presenting a tone sequence monaurally, and, when we wish attention not to be applied to a portion of that sequence, require subjects to perform a competing task in the contralateral ear. Specifically, we present the “galloping rhythm” stimuli of Fig 1 for 21 seconds, and, in some conditions, require subjects to perform a different auditory task in the other ear for the first 10 s. Listeners then revert to making a stream segregation judgement on the tone sequences. In two control conditions the contralateral stimulus is either absent, or is to be ignored. Because stream segregation builds up over time, we can then determine whether the unattended 10 s of the sequence has contributed fully to that build-up. Our results show that it has not, indicating that attention is crucial for the build-up of auditory streaming.

Before describing our first two experiments in more detail, it is worth noting that the build-up of auditory streaming allows us to overcome some of the issues which have complicated the interpretation of visual grouping experiments. For example, Mack et al (1992) presented subjects with a series of trials in which a cross was presented against an unattended background of line segments. On the first two trials all of the line segments had the same orientation, and subjects (reliably) judged which of the horizontal and vertical bars of the cross was longer. On the third trial the line segments in one quadrant of the background had a different orientation from those in the other three. However, subjects were not told this in advance and were instructed to concentrate on judging the cross. When subsequently questioned, they could not identify which quadrant contained the different orientations, even though this task was easy on a later trial in which they were told to attend to the background. Although the authors concluded that the grouping had not taken place in the “inattention” trial, it is also possible that the grouping had occurred, but that subjects either did not attend to the output of that grouping process, or that they did not encode it in memory (c.f Moore & Egeth, 1997). Similar factors confound the interpretation of Joseph et al’s (1997) finding that grouping judgements are impaired for stimuli presented during the “attentional blink” (Raymond, Shapiro, & Arnell, 1992). The problems arise because subjects are required to make a judgement about something to which they are supposedly not attending. There are a number of reasons why they might do badly at such a task, only one of which is a failure of grouping. Our paradigm overcomes this problem by reducing the attention paid to the first half of a sequence but measuring streaming judgements during the second half.

Experiment 1

Method

In all conditions a 21-s sequence of “A” and “B” pure tones, alternating in the “ABA-ABA” sequence as shown in Fig. 1, was presented to the left earpiece of a Sennheiser HD414 headset. Each tone had a duration of 125 ms, was gated on and off with 10-ms linear ramps, and had a level of 55 dB SPL. There was no silent interval between the tones in each triplet, and the silence between the triplets lasted 125 ms (zero-voltage points). The tones were generated digitally with 16-bit resolution, at a sampling rate of 20 kHz, and presented using a WAVjammer (New Media Corporation) sound card installed in a portable PC. All stimuli were calibrated using a B&K artificial ear (type 4153, condenser microphone type 4134) and an HP 3561A spectrum analyser; distortion products were at least 60 dB down. The frequency of the “A” tones was always 400 Hz, and that of the “B” tones was either 4, 6, 8, or 10 semitones higher (504, 566, 635, or 713 Hz).

In the baseline condition, no sounds were presented to the right ear. Subjects received written instructions to the effect that they should press button 1 on the computer keyboard when they heard a galloping rhythm in their left ear, and button 2 when they heard two separate streams. The instructions included an illustration similar to Fig. 1 with the two possible perceptual organisations indicated by dashed lines. Subjects were told to press the appropriate button whenever their percept changed from the “one stream” to the “two stream” representation. A concise reminder of this instruction was displayed on the computer screen throughout the trial.

In the “two task” condition, a series of noise bursts, bandpass filtered digitally (attenuation rate greater than 100 dB/oct) between 2000 and 3000 Hz was presented

to the right ear for the first 10 s of the stimulus. The overall level of each burst, averaged over its entire duration, was 52 dB SPL. The 21-s sequence of tones was presented to the left ear, as in the baseline condition. Each noise burst had a duration of 400 ms, and was labelled either as “approaching” (linear increase in amplitude for 380 ms, followed by 20-ms offset ramp) or “departing” (the approaching burst reversed in time). Subjects were presented with examples of these bursts prior to the experiment, in order to demonstrate the difference between them. In the experiment proper the bursts were presented at an average rate of 1 per second, with a random temporal jitter of +/- 250 ms drawn from a rectangular distribution. Subjects were instructed that, until the noise bursts stopped, they were to ignore the tones in the left ear and to press “A” on the computer keyboard after each “approaching” noise burst, and key “D” after each “departing” burst. Throughout the first 10 s, a concise reminder of this instruction was displayed on the screen. The written instructions stated that, after the bursts stopped, the subjects should switch attention to the left ear and start making the streaming judgement. After 10 s a brief message appeared on the computer screen telling them to switch tasks, at which point the on-screen instructions switched to those for the streaming task. In the “one task with distractor” condition the noise bursts were presented to the right ear as in the two-task condition, but subjects were told to ignore them and to perform the streaming task on the tones in the left ear throughout the 21-s sequence.

Each condition consisted of a single block of 20 trials, with the different B-tone frequencies presented in random order. Six young normally hearing subjects with no history of neurological illness took part. Each performed the three conditions in turn, with the order of conditions counterbalanced across subjects. There were also three practice blocks of eight trials per condition, which were presented in the same order

(baseline, distractor, two-task) for all subjects. This order was chosen so as to familiarise subjects with the set-up, starting with what we expected to be the easiest task to understand and ending with the hardest.

Results

The results of experiment 1, averaged across listeners, are shown for each of the four values of Δf in Fig. 3. Each panel shows the average number of perceptual streams heard as a function of time for a single Δf . In the baseline condition (triangles), it can be seen that the subjects hear a single stream at the beginning of each sequence, with an increased tendency to hear two streams as the sequence progresses in time. This is consistent with the findings of Bregman (1978) and of Anstis and Saida (1985), as is the tendency for the rate of increase to be faster at larger values of Δf . Performance in the “one task with distractor” condition (squares) is very similar to that in the two-task condition.

Crucially, when subjects start performing the streaming task in the two-task condition (after 10 s, circles), they show an amount of streaming that is greatly reduced relative to that in the other two conditions. That is, in the absence of attention, the build-up of streaming was substantially reduced. This was confirmed by a three-way ANOVA on the scores in all three conditions, averaged into 2-s bins from 11 to 19 s. In this and all other ANOVAs described here, the Huynh-Feldt sphericity correction was used, and the uncorrected degrees of freedom reported. The ANOVA showed a main effect of condition ($F(2,10)=7.57$; $p<0.05$), a time X condition interaction ($F(8,40)=4.62$, $p<0.05$), and main effects of time and of Δf . When the ANOVA was performed only on the two-task and one-task-with-distractor conditions, the outcome was similar (condition main effect, $F(1,5)=7.34$, $p<0.05$; condition X

time, $F(4,20)=5.06$, $p<0.05$). Another question concerns the comparison between the amount of streaming in the two-task condition occurring in the second half of the sequence, with that in the other two conditions observed 10 sec earlier. That is, did the competing task *completely* prevent the build-up of streaming? In fact, a three-way ANOVA comparing the streaming in the two-task condition with that occurring 10 sec earlier in the baseline condition just failed to show a significant effect of condition ($F(1,5)=6.25$, $p=0.055$), with no significant interactions. When the time-shifted two-task data were compared with the “one task with distractor” condition, the main effect of condition was far from significant ($F(1,5)=2.15$, $p=0.21$). However, even if these comparisons had proved significant, one could not conclude that some build-up can occur in the absence of attention, because, despite the competing task, it is possible that subjects occasionally paid attention to the tones. The most important conclusion from experiment 1 is that an attentional manipulation can substantially reduce the build-up of stream segregation.

Performance on the contralateral approach/depart task is shown in Fig. 4. These results would have been extremely important if streaming performance in the two task condition had proved similar to that in the other two conditions, as it would have been necessary to demonstrate that subjects were deploying some attentional resources to the contralateral noise bursts. The data show that four of the six subjects performed better than the 95% confidence limit (shown by the upper dashed line) above chance performance (50%). Two subjects performed below the lower 95% limit, possibly due to them having confused the labels to be applied to the approach and depart stimuli.

Discussion

The results of experiment 1 provide evidence that attention is crucial for the build-up of auditory streaming. Note that this differs from the finding that, at intermediate frequency separations and presentation rates, listeners can choose whether to focus on a “one stream” or a “two stream” percept (van Noorden, 1975). One could easily attribute this earlier finding to the streaming mechanism producing two outputs of roughly equal strength, and to attention being able to select one or other of these representations more or less at will. Rather, we believe that our results implicate attention in the streaming process itself. In the General Discussion section we consider the extent to which this conclusion is likely to apply to other auditory grouping principles, and its implications for models of stream segregation that are based on peripheral auditory processes (e.g. Beauvois & Meddis, 1991; Beauvois & Meddis, 1996).

It is of course important to rule out alternative explanations for our results. One of these is suggested by the results of Rogers and Bregman (1993), who showed that presenting a series of contralateral tones reduced the build-up of auditory streaming. In their study the tones were selected so as to disrupt the temporal pattern of the ipsilateral tones, and they interpreted their results in this way. Such an explanation cannot however account for the effect our contralateral noise bursts, whose frequency region and stochastic properties ensured that they would fall into a separate auditory stream from the ipsilateral tones. Furthermore, of course, the noise bursts had no effect when subjects were instructed to ignore them. A second explanation may be that subjects had a bias to respond “one stream” shortly after switching tasks in the two-task condition. Specifically, because in the other conditions they were used to responding “one stream” at the beginning of each trial, they may have become used to making such a response whenever they started making streaming judgements. To test

this explanation, experiment 2 included a condition in which subjects attended to the tone sequence throughout its entire duration, but switched from another task to the streaming task halfway through.

Experiment 2

Method

The subjects, the method of signal generation, and the basic procedure were the same as in experiment 1. However, no sounds were presented to subjects' right ear in experiment 2. The tone sequences presented to the left ear were the same as in experiment 1, except that each tone was sinusoidally amplitude modulated by 100% at a rate equal to either 8 Hz ("slow rate") or 16 Hz ("fast rate") of its carrier frequency. Each sequence started at either the fast or slow rate at random, and the probability that the modulation rate would switch between any two consecutive tones was 0.1. This led to a switch occurring, on average, about 4 seconds after the previous switch. The modulation was present in both conditions of this experiment. Its purpose was not to affect the streaming process, but rather to give the subjects another task to perform in one of the conditions, whilst still requiring them to attend to the tones.

In the one-task condition, subjects were told to ignore the modulation and make the streaming judgement throughout the 21-s sequence. In the two-task condition the written instructions told them to perform a modulation discrimination task for the first 10 s, by pressing key "S" when they heard a slow modulation, and key "F" when they heard a fast modulation. They were not required to respond to every tone, but were told to change their response as often as the modulation rate changed. The instructions stated that about halfway through the sequence, after 10 s, they would be required to

switch to the streaming task. The message on the computer screen reminded them of the response requirements for the modulation task during the first 10 s, after which a message appeared telling them to switch strategies and the instructions on the screen changed accordingly. Subjects received two practice blocks, with twenty trials per condition, with that for the one-task condition occurring first. They were also played demonstrations of tones with the slow and fast modulation rates. In the main experiment, the order of conditions was counterbalanced across subjects.

Analysis of performance in the AM rate discrimination task was complicated by the fact that there was a delay between listeners noticing that the AM rate had changed and them pressing the appropriate key. We tried measuring performance assuming a number of values for this delay, and observed that the highest scores were obtained when a delay of 2 s was assumed. The data for the first 8 s of the sequence in the “two task” condition were analysed using this assumption, with the responses for each subject and condition placed in 0.5-s bins.

Results

Each panel of Fig. 5 shows the mean number of auditory streams as a function of time for one value of Δf . As before, streaming builds up over time, with a tendency for the rate of this build-up to be faster at wider frequency separations. Importantly, however, and in contrast to the results of experiment 1, the results of the one-task (squares) and two-task (circles) conditions are now very similar to each other. Evidence that subjects were reliably performing the AM discrimination task in the first part of the two-task condition is provided by Fig. 6, which shows that all except one performed significantly above chance.

The results of experiment 2 show that, although subjects switched tasks half-way through the two-task condition, streaming had built up to a level that was

statistically indistinguishable from that in the one-task condition. This was confirmed by a three-way repeated-measures ANOVA on the data in 2-s bins centered on times between 11 and 19 s. Although there was a main effect of Δf ($F(3,15)=9.18$, $p<0.01$), neither the main effect of condition ($F(1,5)=1.46$), nor the condition X time interaction ($F(4,20)=0.27$) was significant. Furthermore, when the data in the two-task condition were shifted back in time by 10 s, they fell significantly above those in the first 10 s of the one-task condition ($F(1,5)=39.35$, $p<0.01$), confirming that streaming had indeed built up during the two-task condition. We interpret the different pattern of results in the two-task conditions of experiments 1 and 2 to the fact that, during the first 10 s of each trial, subjects attended to the left-ear tones in the second but not the first experiment.

Experiment 3

The first two experiments demonstrated that attention plays an important role in the formation of auditory streams. The involvement of such a high-level cognitive process argues against accounts of the build-up of stream segregation in terms of peripheral auditory processes (Anstis & Saida, 1985; Beauvois & Meddis, 1991), and indicates a role for more central neural structures. A perhaps more direct method of constraining the potential neural bases of stream segregation is to study patients with brain lesions. In our final two experiments we study stream segregation for stimuli presented to the left and right ears of patients with right-hemisphere lesions following strokes. Specifically, we compare the results on an auditory task, of stroke patients exhibiting unilateral neglect to left-sided visual stimuli, with those of other patients with right-hemisphere lesions and of healthy aged-matched controls. One reason why

neglect patients may differ from the control groups is suggested by the effect of attention on the build-up of stream segregation, as shown in experiments 1 and 2. Given the evidence that neglect is supra-modal (e.g. Bisiach, Cornacchia, Sterzi, & Vallar, 1984), and reflects attentional rather than sensory mechanisms (for reviews see Halligan and Marshall, 1993 and Rafal, 1998), one might expect less build-up of streaming for sounds presented to the left than to the right ears of neglect patients. No such asymmetry would be predicted for the control groups, whose results might be expected to resemble those obtained with stimuli presented to the right ear of neglect patients.

Mechanisms by which neglect might affect stream segregation are discussed in the final section. Here we note that, even though the patients in this study are selected on the basis of their symptoms rather than on the site of their lesions, such a finding would impose several constraints on the neural mechanisms involved in streaming. It is also worth pointing out that in hearing, even more so than in vision, information on which neural structures or networks are involved in grouping is extremely sparse (for an exception, see Scheich *et al.*, 1998). Hence even the ability to distinguish between brainstem and more central structures would represent something of an advance.

Methods

All subjects listened to 6-s sequences of repeating triplets of “ABA” tones similar to those used in experiments 1 and 2 (Fig. 1). As before, the frequency of the A tones was fixed at 400 Hz and that of the B tones differed across trials. Six different frequencies of the B tones were used, consisting of the four used in experiments 1 and 2 plus one smaller (449 Hz, $\Delta f=2$ semitones) and one larger value (800 Hz, $\Delta f=12$ semitones). Each subject was tested on four blocks of 24 trials, each consisting of four

repetitions of each of the six values of Δf in random order. Stimuli in the first and last blocks were presented to one ear, whereas those in the middle two blocks were presented to the other. The choice of the ear to be tested first was counterbalanced across subjects; post-hoc analyses revealed no differences between the first and second block of trials for a given ear.

Initial testing using the method of experiments 1 and 2, in which subjects “tracked” changes in the percept throughout each sequence, revealed that the neglect patients had difficulty in disengaging from their first response, and rarely made any subsequent responses throughout the trial. This occurred regardless of whether the sounds were played to the left or right ear, and is consistent with other findings showing that neglect is associated with non-spatial difficulties sustaining attention over time (Robertson *et al.*, 1997), as well as with attending differentially to stimuli separated only in time and not in space (Husain, Shapiro, Martin, & Kennard, 1997). We therefore adopted a different method in which subjects were asked, at the end of each trial, which of the two possible percepts (one stream or two) was heard throughout most of the sequence. The stimuli were presented at a level of 67 dB SPL over Sennheiser HD414 headphones.

Three groups of subjects took part. One group consisted of four subjects exhibiting unilateral neglect, whose details are shown in Table 1. All of these were classified as suffering from unilateral neglect on the Behavioural Inattention Test (“BIT” Wilson, Cockburn, & Halligan, 1987) on the basis of screening for an earlier study (manuscript in preparation). As a check for any recovery from the symptoms of neglect, we re-tested the four patients after the end of experiment 3 on two components of the BIT – namely, the line bisection and star-cancellation sub-tests. The resulting scores are shown in Table 1, and reveal that, although three of our

patients fell outside the normal range, one of them (SH) did not. This patient might therefore be best considered as at least partially recovered. As it turned out, of all the patients in our neglect group, SH showed the pattern of results most similar to that of the controls. However, it was decided not to exclude him from our analyses on these post-hoc grounds.

Following the streaming experiments the thresholds in quiet for a 500-ms 600-Hz tone were measured for three patients using a two-interval forced-choice procedure and the “QUEST” adaptive procedure, which converges on the 92%-correct point on the psychometric function, described by Watson and Pelli (1983). Two of these showed higher thresholds in the left than in the right ear, which suggested that they might have an asymmetric sensory or conductive deficit. However, it may also be that they had difficulty in maintaining attention throughout the two-interval trial, and so we repeated the absolute threshold measures on these two patients using a one-interval (yes-no) procedure.¹ The resulting thresholds did not differ between the two ears, suggesting that the asymmetry observed with the two-interval task was not due to a peripheral deficit. Unfortunately, patient SH is now deceased. At the time of his death, we had not measured his absolute thresholds.

A second subject group consisted of four patients with right-hemisphere lesions, but who did not exhibit any signs of unilateral neglect. Their mean age was 54 years, and details of their lesions are provided in Table 2. The third group consisted of six healthy age-matched (mean age = 67 years, range 61 to 70) controls with no history of brain dysfunction. No subject in either of the control groups made any errors on the star cancellation test, and all fell within the normal range on line bisection.

Results

Figure 7a shows the proportion of trials in which subjects reported hearing two streams as a function of Δf , with each curve showing the average for stimuli presented to either the left or right ear of one subject group. Roughly speaking, five of the six curves overlap, with the exception being that for stimuli presented to the left ears of the neglect patients. Hence the neglect patients (“R+N+”) show less stream segregation for stimuli presented to their left than to their right ears, whereas no such asymmetry occurs for the controls with (“R+N-”) or without (“R-”) right-hemisphere damage. This finding was confirmed by two separate ANOVAs. First, a two-way repeated-measures ANOVA performed solely on the data from the neglect patients revealed a main effect of ear of presentation ($F(1,3)=10.77$; $p<0.05$). This effect interacted significantly with Δf ($F(5,15)=5.55$, $p<0.01$), reflecting the floor and ceiling effects at the smallest and largest frequency separations tested. Not surprisingly, there was also a main effect of Δf ($F(5,15)=44.31$, $p<0.001$). Second, the differences between the left- and right-ear scores of each subject at each Δf were subjected to a two-way ANOVA with one between-subjects (group) and one within-subjects (Δf) factor. There was a main effect of group ($F(2,11)=7.22$, $p<0.01$), due to the larger ear asymmetry in the neglect patients. This analysis allowed us to perform planned comparisons, which revealed that the asymmetry shown by the neglect patients was significantly greater than that of either the non-neglect brain-damaged group ($F=12.94$, $df=1$, $p<0.01$) or the age-matched controls ($F=8.98$, $df=1$, $p<0.05$). The ANOVA also showed a main effect of frequency, reflecting the absence of asymmetry at those (extreme) values of Δf where scores were at floor or ceiling.

An indication of the variation across listeners is provided by Fig. 7b, which shows the difference between the left- and right-ear streaming scores, averaged across

Δf , for each individual listener. All of the neglect patients showed more stream segregation in their right than in their left ears, and only one other subject (an age-matched control) showed data falling within the range of the neglect patients. The neglect patients in Table 1 are ordered in terms of the size of the ear asymmetry, with DEN showing the largest effect and SH the smallest.

The results of experiment 3 are consistent with the effects of attention on auditory streaming that were demonstrated in the first two experiments. Although we believe this to be the most parsimonious interpretation of the results, alternative explanations will be considered in the Discussion section. Generally speaking, we will argue that these alternatives are unable to account for our data. There is however one possible explanation which would render trivial the results of experiment 3, and the purpose of experiment 4 was to control for this. It is known that neglect patients have difficulty in sustaining attention to sounds presented at midline (Robertson *et al.*, 1997), and it is possible that this difficulty is exacerbated when stimuli are presented to the left ear. If so, then it could be that the neglect patients were basing their responses only on the beginning of each 6-s left-ear sequence. Given the tendency of streaming to build up over time, this would in turn lead to a reduced tendency to report hearing two streams. If so, the results of experiment 3 would not demonstrate that the streaming process itself was impaired by neglect, but, rather, would reflect a tendency of neglect patients to analyse only that portion of the sequence where streaming has not built up even for normal subjects.

Experiment 4

Method

In the first three experiments the frequency separation (Δf) between the A and B tones remained constant throughout each trial. In contrast, experiment 4 used sequences in which Δf either increased or decreased throughout each sequence. If the neglect patients base their responses on the beginning of each trial, then they should report less streaming for a sequence in which Δf is initially small and gradually increases (Fig. 8a, solid line) than for one in which it starts off large and gradually decreases (dashed line). To test this, two of the neglect patients of experiment 3 (DDN and CGR) and six age-matched controls listened to sequences in which Δf decreased or increased quasi-linearly by two semitones throughout each 6-s sequence (Fig. 8a). We use the term “quasi-linearly” because no frequency glides were imposed on the tones, and so the change in Δf was not, strictly speaking, continuous. The frequency of the A tones was constant at 400 Hz, and that of each B tone was defined as the position of the linear trajectories shown in Fig. 8a at the temporal centre of that tone. The mean Δf in each sequence was, in separate conditions, 3, 5, 7, 9, and 11 semitones. All subjects listened through their left ear and were tested on two blocks of 20 trials, with the order of conditions within each trial completely randomised. In all other respects the method was the same as in experiment 3.

A prediction of experiment 4 is that, if neglect patients were not applying a disproportionate weight to the beginning of each sequence when making their responses, then there should be no difference in their streaming judgements of “increasing Δf ” and “decreasing Δf ” sequences. However, the lack of such a

difference could be due to the range of Δf spanned in each sequence being insufficiently wide. In order to test whether a difference would be observed even if subjects were just attending to the beginning, the aged-matched controls were also presented with the first 3 s of the decreasing- and increasing- Δf sequences. Four blocks of twenty trials were run. This part of the experiment was performed after the main part, so that participation in this condition would not affect performance of the control subjects in the first part.

Results

The results of experiment 4, averaged across Δf and across the subjects within each group, are plotted in Fig. 8b. The difference between the number of streams reported for the increasing- and decreasing- Δf conditions by the neglect patients (“wholes, R+N+”) was close to zero, as shown by the fact that the right-most bar is barely distinguishable from the abscissa. Note that the absence of a difference was not due to floor or ceiling effects: the mean number of streams reported, averaged across conditions, was 1.43 for patient CCR and 1.5 for patient DDN. There was a small effect for the control subjects when they were presented with the entire 6-s sequences (“wholes, R-” middle bar), but this just failed to reach significance (2-way ANOVA, $F(1,5)=6.04$, $p=0.057$). Furthermore, presenting the controls with the first half of each sequence (“halves, R-” left-most bar) did result in a significant difference in streaming judgements ($F(1,5)=35.7$, $p<0.01$). Overall, the results show that listening to the beginning of each 6-s sequence would produce a difference between the increasing- and decreasing- Δf conditions, but the neglect patients did not show any such difference. A *caveat* to this conclusion arises from the fact that only two neglect patients participated in experiment 4, and so the lack of a significant difference

between the “increasing Δf ” and “decreasing Δf ” conditions for this group might be due to a lack of statistical power. However, we should note that the difference between the two conditions was very close to zero, and so it is hard to imagine that the addition of the other two neglect patients would have resulted in a significant finding. Furthermore, it is not the case that the significant results of experiment 3 were dependent on the two neglect patients who did not take part in experiment 4. When the analysis of the left-right differences in experiment 3 was repeated with those two patients removed, the significance of the main findings persisted (main effect of group, $F(2,9)=4.82$, $p<0.05$; planned comparisons, $d.f.=1$: neglect vs. right-brain-damaged, $F=9.54$, $p<0.02$, neglect vs. age-matched, $F=5.81$, $p<0.05$).

General Discussion

The effects of attention on streaming and other grouping phenomena

The results presented here clearly demonstrate the importance of attention for the build-up of auditory stream segregation. As was noted in the discussion of experiment 1, this is a qualitatively different finding to the observation that the listener’s attentional set can influence whether that person reports hearing one or two streams (van Noorden, 1975). By showing that attending to one part of the sequence has an effect on the stream segregation of a later part, experiment 1 allows us to rule out the possibility that our manipulation merely affected the interpretation of the output of the streaming process. Rather, we argue that attention is crucial for the streaming process *per se*. A related conclusion was reached by Brochard, Drake, Botte, and McAdams (1999). They required subjects to detect an irregularity in a temporal sequence of tones, in the presence of one, two, or three other sequences,

where the tones in each sequence had a fixed frequency which was different to that of the other sequences. Attention was focussed on the target sequence by playing an example of it (without the irregularity) before each mixture. Performance did not deteriorate as the number of additional sequences was increased beyond one, leading Brochard *et al* to suggest that the additional “non attended” sequences were not being organised into streams. They argued that the organization of these additional streams would have increased the amount of processing required of the subjects, and should therefore have reduced performance. However, they did acknowledge that their data did not allow them to differentiate between this explanation and the view that streams are formed automatically, even when the components of those streams are unattended.

A different conclusion was reached in two articles by Sussman, Ritter, and Vaughan (1998; 1999), who measured the mismatch negativity (“MMN”) component of the auditory evoked potential in response to tone sequences. The MMN is a negative wave that occurs in response to an “oddball” stimulus presented in a sequence of otherwise homogenous stimuli, and has been observed even when subjects are not attending to the stimuli (Cheour-Luhtanen *et al.*, 1996; Kane *et al.*, 1996; Näätänen, Paavilainen, Tiitinen, Jiang, & Alho, 1993). They presented subjects with a sequence of tones that alternated regularly between a high and a low frequency range, with the tones in each range playing a simple melody. On a minority of trials they altered the order of the tones in the low range, and argued that this should elicit an MMN only when the “interfering” high-frequency tones were pulled into a separate auditory stream. (It is known that interleaving notes from a distracting melody with those of a target melody impairs recognition of the target, and that this interference is much greater when the target and interferer form part of the same stream: see e.g. Hartmann & Johnson, 1991). They found that, when the tones alternated at a slow

rate, an MMN was generated only when subjects attended to them; in contrast, at fast rates - more similar to those used here - an MMN was observed even when subjects were told to ignore the tones and to read a book. They concluded that attention was necessary for streaming at slow but not at fast rates.

One of the many differences between Sussman *et al*'s work and our own lies in the extent to which attention was diverted away from the tone sequences. Although in one condition of their experiments subjects were told to read a book and to ignore the tones, it was nevertheless the case that the tones were the only sounds present in the experiment. This fact, combined with evidence that auditory and visual attention are to some extent independent (Duncan, Martens, & Ward, 1997), suggests that some auditory attentional resources were allocated to the tone sequences. This stands in contrast to the "two task" condition of our first experiment, which required subjects to perform an exacting auditory task on stimuli presented to the contralateral ear. One possibility is therefore that streaming does require attention even at fast rates of alternation, but that the attentional manipulation needed to observe this is more rigorous than simply asking the subjects to ignore the tones. A similar point has been made by Nakayama and Joseph (1998), who argued that attention is important even for "easy" visual search tasks, and that evidence to the contrary was based on experiments in which attention to the stimuli was insufficiently reduced. It is also worth noting that, although the MMN is generally thought to reflect pre-attentive processing, the results obtained by Sussman *et al* (1998) with sequences that alternated at a slow rate indicates that the MMN can be affected by attention (see also Alain & Woods, 1994; Näätänen *et al.*, 1993)². Finally, Schröger (1998), has warned that, even though the MMN can be observed in some tasks where attention is directed

away from the test stimuli, care must be taken when interpreting the existence of an MMN in any particular task in terms of the attentional resources needed for that task.

Streaming, attention, and localization

An additional line of evidence that the streaming of sequential sounds occurs at a fairly central level of processing comes from the effects of cues to perceived location, and in particular of interaural time and level differences (“ITDs” and “ILDs”, respectively). There is now a wealth of evidence these cues have little or no influence on the grouping of simultaneous frequency components into one or more auditory objects, at least in the absence of additional cues to segregation. The lack of an effect of ITDs has been shown for the integration of components into the pitch of a complex sound (Hill & Darwin, 1996), and of different formants into the phonetic identity of a vowel (Culling & Summerfield, 1995). Analogous null results have been reported for ILDs in the detection of mistuning (Gockel & Carlyon, 1998) and in the extraction of pitch (Beerends & Houtsma, 1989). However, in tasks where the stimuli to be streamed are spread out over time, the results are rather different. Of particular relevance here is the finding that the build-up of streaming in a monaural sequence is reduced when the first part of that sequence is played diotically (Rogers & Bregman, 1993). This result, which shows that the build-up can be reduced without altering the physical stimulus to the “test ear”, demonstrates that it must be mediated by processes which receive an input from binaural mechanisms, presumably those involved in the perception of location. Other paradigms in which an effect of ITDs and/or ILDs have been observed include picking out one tune from a pair of interleaved melodies (Hartmann & Johnson, 1991), and tracking one spoken message in the presence of another (Darwin & Hukin, 1999).

The distinction between simultaneous and sequential grouping processes may also prove important when evaluating the effects of attention. The above discussion has described three tasks – streaming, interleaved melodies, and tracking a message – which are influenced by perceived location. It is interesting to note that all three of these can be thought of as involving attention. Hence, although we have demonstrated an influence of attention on a sequential streaming process, it is by no means certain that this is the case for simultaneous grouping cues. For example, widely separated frequency components of a sound are perceptually fused when they are turned on and off together very quickly, as shown by the perception of a click as a single entity, and by the large amounts of masking produced by such synchronous components (Carlyon, 1989). It seems unlikely that attention could be directed to a click fast enough to influence the grouping process. Hence it seems that either the common onset cue does not require attention, or that all non-attended sounds (even those presented at different times) are fused by default into a single percept, with attention being required for any segregation to take place.

A related question, which also concerns the relationship between attention, localisation, and streaming, arises from the nature of our competing task. Because all of the competing noise bursts were presented to the contralateral ear, our results do not differentiate between subjects failing to attend to a particular location, and failing to attend to an auditory object. (Similar distinctions are drawn in accounts of visual attention - e.g. Duncan, 1984). In other words, would the results of experiment 1 have been substantially different if the noise bursts had been presented to the same ear as the test tones? Experiments investigating this and other issues concerning what types of distracting task can inhibit the build up of streaming are currently underway in our laboratory.

Constraints on potential neural loci of auditory streaming

As discussed above, the effects of perceived location on the build-up of streaming (Rogers & Bregman, 1993) suggest that streaming mechanisms receive an input from binaural processes. This in turn suggests that central auditory mechanisms are involved in the streaming process itself, rather than just affecting the interpretation of the output of those processes. Further evidence for this comes from the results of experiment 3, which showed that neglect patients show reduced streaming of stimuli presented to their left ear, compared both to stimuli presented to their right ears and to those presented to either ear of the controls. Even if the right-hemisphere strokes which caused the neglect had co-incidentally damaged peripheral structures, something we consider unlikely, then this should have reduced streaming of stimuli presented to their right ears. The fact that the neglect patients showed reduced streaming on the left means that the finding must be due to damage at a site at which the majority of excitatory connections have crossed to the contralateral side of the brain. Our results are also unlikely to be due to damage to the inferior colliculus (IC, in the auditory midbrain), which is largely served by a different arterial circulation (basilar artery/ posterior cerebral) than that providing the blood supply to the main lesion sites of our patients (middle and anterior cerebral arteries, with the exception of the very posterior portion of the parietal lobe and the medial face of the temporal lobe). In addition, there is no reason to suppose that our control brain-damaged patients without neglect would have suffered less damage to the IC than did our neglect patients.

Overall, then, the results of experiment 3 point to a cortical involvement in the streaming process. The effects of attention observed in experiment 1, combined with the fact that the neglect subjects were selected on the basis of their attentional

impairment (rather than on lesion site), make it tempting to conclude that results of experiment 3 were due to damage to cortical attentional processes. However, it is important to consider alternative explanations for those results. One such alternative was ruled out by experiment 4; others are discussed below.

Reduced streaming for stimuli presented to the left ears of neglect patients

One obvious way in which neglect could result in a different pattern of results between stimuli presented to the left and right ears would occur if it caused patients to be unsure of what they had heard. For example, neglect patients may be unaccustomed to making judgements about sounds presented on the left, because these are often concurrent with, and “extinguished” by, competing sounds on the right (e.g., de Renzi, Gentilini, & Barieri, 1989). If this were the case, one would expect the function relating the number of streams heard to Δf to have a shallow slope; in other words, if they were just guessing then there is no reason to expect the proportion of “two stream” responses to vary with Δf . Inspection of Fig. 7a shows that this was not the case, with portions of that function (for example between $\Delta f = 8$ and 10 semitones) being at least as steep as those for the neglect patients’ right ears or for control subjects. An interesting corollary of this is that it shows that neglect has caused a qualitative difference in the perception of sounds in the left vs. right ear. This differs from previous studies of auditory neglect, which have generally shown either performance that was closer to chance in the left than in the right ear (de Renzi *et al.*, 1989; Soroker, Calamaro, Glickson, & Myslobodsky, 1997), a difference in perceived location (Bisiach *et al.*, 1984; Vallar, Guariglia, Nico, & Bisiach, 1995), or a non-lateralized deficit (Cusack, Carlyon, & Robertson, 2000; Robertson *et al.*, 1997). However, we should note that the neglect patients did not spontaneously report any

difficulty in segregating sounds presented on the left-hand side of space. One reason for this may be that it is fairly rare, in everyday life, to be presented with two competing sources both of which are strongly localized to the same side.

Another possibility is that the stimuli sounded somehow less clear when presented to the neglect patients' left ears, and that this reduced the probability of subjects reporting the existence of two streams. There are three reasons why this is unlikely to provide an explanation for our results. First, unilateral sensory hearing loss, which degrades both the frequency and temporal resolution of sounds presented to one ear, does not result in a consistent streaming difference between the two ears (Rose & Moore, 1997). Second, although it is conceivable that some more severe form of unilateral degradation of auditory processing could occur as a result of stroke, we have no reason to believe that the primary auditory structures of our neglect patients (with the possible exception of subject CGR) are damaged. Finally, if streams were formed at a peripheral level, and damage to, say, auditory cortex blurred the representation of these streams, this would not necessarily lead to a change in the number of streams reported: the streams which subjects hear might sound blurred, but the number of streams should be unaffected.

Implications for theories of auditory of stream segregation

The results presented here have implications for two different classes of theory of auditory stream segregation. The first of these, proposed by Bregman (1990), invokes the Gestalt principles of perceptual grouping and is consistent with the operation of higher cognitive processes. For example, Bregman proposes that the auditory system starts off with a 'default' assumption that all sounds belong to the same stream, and segregation builds up as a result of a process of "evidence

accumulation”. His approach focuses on the general principles that the system might use, and on the types of problem with which it is faced, rather than on proposing specific mechanisms which might be used to perform those tasks. Clearly, the idea that attention is important for the evidence-accumulation process is not a hard one to countenance, and so our findings could be incorporated within this general framework. However, as noted in the Introduction, Bregman has explicitly argued that the formation of auditory streams occurs even when subjects are not attending to the elements of those streams, and so this aspect of his theory would have to be modified.

More recently, a number of models have been proposed, which, in addition to specifying in some detail the nature of the mechanisms underlying streaming, generate quantitative and testable predictions (Beauvois & Meddis, 1991; Beauvois & Meddis, 1996; Brown & Cooke, 1998; McCabe & Denham, 1997). An influential model of this type, proposed by Beauvois and Meddis (1991; 1996), successfully accounts for a number of streaming phenomena, including the build-up over time shown here and elsewhere (Anstis & Saida, 1985; van Noorden, 1975). They propose that, following peripheral filtering and auditory-nerve adaptation, the output of each frequency channel is temporally smoothed, subjected to a cumulative random bias proportional to the level of activity in that channel, and then undergoes a second smoothing. The excitation levels in the different channels are compared every 1 ms, and that in all but the “dominant” channel (the one with the most excitation) are attenuated. This “vicious circle”, in which the suppression of a non-dominant channel increases the probability that it will be suppressed in the future, results in the build-up of segregation. For a two-tone sequence, streaming is said to occur when the response to one of the tones exceeds the response to the other one by a given ratio, Z_t . Importantly, Beauvois and Meddis argue that all of the processes in their model have

properties similar to those of the auditory periphery, and discuss their results entirely in terms of the cochlea, auditory nerve, and auditory brainstem. In general, it is possible that processes operating at the level of the brainstem could be affected by attention. However, the results of experiments 1 and 2 suggest that this would require a crucial descending pathway which essentially “turned on” the process of segregation only when attention was being deployed. Because Beauvois and Meddis’s model rests on “automatic” processes (peripheral filtering, auditory nerve adaptation, and temporal smoothing), it is hard to envisage how these could be mediated by descending pathways. An exception is the parameter Z_t , which could be viewed as a criterion value applied by a central decision mechanism. This could account for the fact that the instructions given to a subject can, by affecting this decision criterion, influence the number of streams that are reported listener reports (van Noorden, 1975). However, it seems much less plausible that it could account for the effects of attending to the first half of a sequence on the streaming perceived in the second half. To do so, it would have to propose that the criterion was affected by having performed another task some seconds earlier (experiment 1), and that no such effect occurred when the competing task was performed on the objects that were to be streamed (experiment 2). Similar arguments apply to the effects of top-down influences on the criterion value of the “attentional searchlight” which forms the final stage of Brown and Cooke’s (1998) neural oscillator model of auditory streaming.

An alternative “data driven” model has been developed by McCabe and Denham (1997). They proposed two arrays of neurons responding to the “foreground” and “background” streams respectively, with mutual inhibition between the two. (The foreground stream is the one which is most perceptually salient at a given time). In order to account for the experimental results, this inhibition had to decay with a time

constant of 600 ms, which they considered to be more consistent with cortical than with peripheral auditory processes. However, although they included a potential “attentional input” to their model, this was not used in their simulations and took the form of a non-specified input to the foreground array. Because the form of the input was not specified, it is not obvious how it could account for the results of experiment 1. A more promising approach is suggested by the fact that the build-up of streaming in their model is dependent on the inhibitory interaction between the two streams. It is possible that descending influences from attentional mechanisms could act as a gate on these inhibitory interactions, turning them on only when attention was directed to the sequences.

Summary, speculations, and future directions.

The two pairs of experiments described here investigated auditory streaming using quite different approaches, the results of which converge on the conclusion that high-level cognitive processes, and specifically attention, are crucial for the build-up of auditory stream segregation. We cannot conclude that there are no circumstances under which unattended tone sequences would split into two streams, but our results do demonstrate that attention has a large effect that cannot be characterised as simply affecting the interpretation of the output of the streaming process.

The implications of our results for peripherally-based models of stream segregation have already been discussed in some detail. It is worth considering at this point potential mechanisms by which unilateral neglect might affect streaming. One possibility, which follows from our discussions of auditory models, is that a descending input from high-level attentional processes may be needed to “turn on” the

streaming process. If this input were inactivated or damaged in neglect, then reduced stream segregation would result. According to this scenario, then, although attention was not sufficiently compromised to prevent accurate judgements to left-sided stimuli (as evidenced by the steep functions in Fig. 7a), the deficit could still have an effect on the qualitative perception of those stimuli. An alternative possibility is that the neural mechanisms responsible for streaming, although receiving input from the auditory pathway, actually reside in those structures of the brain involved in attention and affected by neglect.

Finally, it is worth noting that the paradigm used in experiments 1 and 2 has two potential applications in visual and cross-modal studies. First, Anstis, Giaschi, and Cogan (1985) have shown that an analog of the build-up of stream segregation occurs in the visual domain. They presented subjects with a spot which jumped back and forth between two positions, and identified conditions under which the percept changed from a single moving source (“apparent motion”) at the beginning of the sequence to two discrete flickers at the end. One approach would be to determine whether this “build up of visual stream segregation” was reduced by a competing task. Second, there has been some debate in the literature concerning the independence of visual and auditory attention (Arnell & Jolicoeur, 1999; Duncan *et al.*, 1997). Evidence on whether a visual task prevented the build-up of auditory streaming (or vice versa) would provide a significant contribution to this debate.

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Footnotes

¹ Strictly speaking, there are problems associated with using an adaptive procedure with a one-interval task. These include the fact that the subject's response criterion might change throughout the procedure. However, we were interested in the asymmetry between ears and assumed that any such effects would not differ between stimuli presented to the left and those presented to the right. The method of constant stimuli was not used because of time constraints.

² Näätänen *et al* (1993) observed effects of attending to a competing task in the contralateral ear on the MMN for the detection of changes in intensity, but not in frequency. Relevant to our discussion is the fact that no reduction in the MMN was observed (even for intensity changes) when subjects were simply told to ignore the auditory stimuli compared to when they were told to attend to them.

Table 1

Initials	Lesion	Post CVA (months)	Age	Line Bisect	Star Cancellation	2IFC		Yes/No	
						L	R	L	R
DEN	P,t,o (f)	24	70	5	53	11	11		
DDN	no scan	21	73	0	46	39	29	13	15
CGR	F,p,t	34	58	6	24	24	19	24	23
SH	F,t, (p)	27	71	8	54	(deceased)			

Note Details of the four neglect patients who participated in experiment 3. The main lesion site is given in capital letters, with other affected areas given in lowercase (p=parietal, t=temporal, o=occipital, f=frontal). Where the involvement of an area is questionable it is given in parentheses. Note that CGR's lesion included parts of auditory cortex.

The normal range for the line bisection task is 8-9, and that on the star cancellation task is 52-54. Although SH is inside the normal range on these two neglect tests, administration of the full BIT test in earlier testing 12 months previously indicated neglect.

Table 2..

Initials	Aetiology	Post-onset (months)	Age
NB	CVA (infarct, ant. Sylvian region))	12	63
QQ	(frontal lobectomy)	28	51
TI	CVA (infarct?, temporo-parietal)	75	43
KQ	CVA(infarct, ant horn/body lateral ventricle)	76	60

Note Details of the right-brain-damaged controls who participated in experiment 3. Note that although subject TI's lesion involved the temporal and parietal lobes, she exhibited no signs of unilateral neglect or sensory loss on clinical examination or on the star cancellation task

Figure legends

Figure 1. Schematic representation of van Noorden's (1975) "galloping rhythm" stimulus used in the instructions for experiments 1 and 2. The dashed lines in parts a) and b) of the Figure demonstrate the perceptual organisations corresponding to one and two streams respectively.

Figure 2. Schematic of the stimuli used by Bregman and Rudnicki (1975). a) Target tones only b) Distractor tones ("X") are added, c) Distractors are captured into a separate stream by the "C" tones

Figure 3. Scores are averaged across listeners and repetitions, and are smoothed with 0.5-s bins for the baseline (triangles), two-task (circles), and one-task-with-distractor (squares) conditions. Listeners took a finite amount of time to start responding at the beginning of each streaming task (e.g. after 10 s in the two-task condition and 0 s in the others); data are only plotted for those points where at least half of the possible responses had been made.

Figure 4. Proportion of correct responses on the contralateral distractor task in experiment 1. The 95% confidence intervals surrounding chance performance are shown by dotted lines. The standard error is shown separately for each subject

Figure 5. Each panel shows the number of auditory streams heard for one value of Δf in experiment 2 as a function of time. Each curve shows the responses smoothed with 0.5-s bins for the one-task (squares) and two-task (circles) conditions. Subjects took a finite amount of time to start responding at the beginning of each streaming task (e.g.

after 10 s in the two-task condition and 0 s in the one-task condition); data are only plotted for those points where at least half of the possible responses had been made.

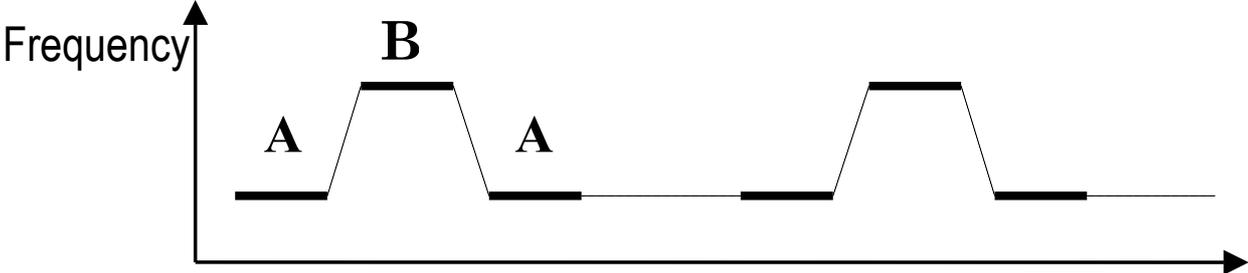
Figure 6. Proportion of correct responses on the AM discrimination task in one condition of experiment 2. The 95% confidence intervals surrounding chance performance are shown by dotted lines. The standard error is shown separately for each subject.

Figure 7 a). Mean proportion of streams heard as a function of Δf by the neglect (squares), aged-matched controls (triangles) and control patients with right-hemisphere damage (circles) of experiment 3. Points joined by dotted and by solid lines are for stimuli presented to the left and right ear respectively. b). Difference between the average number of streams heard in the right and left ears by the individual subjects of experiment 3. Note that the neglect patients in Table 1 are ordered so that DEN showed the largest right-left difference and SH the smallest. When describing subject groups, the abbreviations R+ and R- are used to describe those with and without right-hemisphere damage, and N+ and N- those with and without neglect.

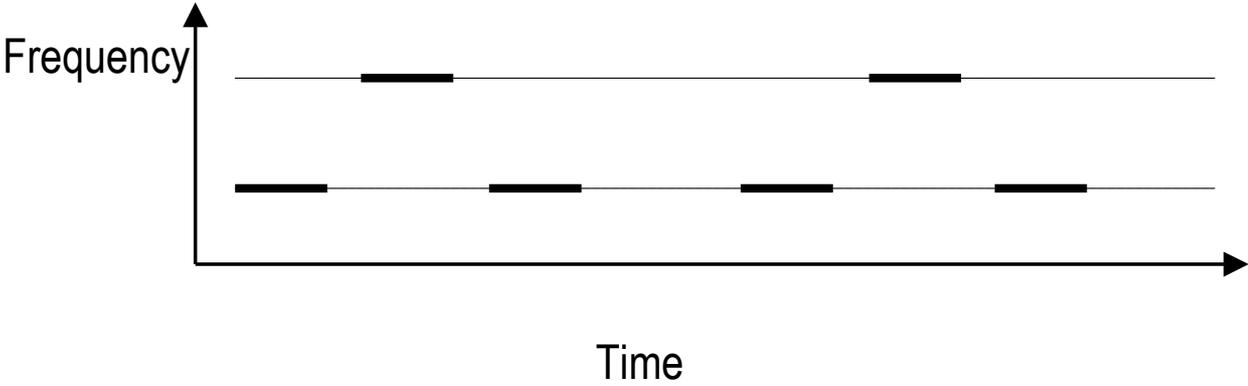
Figure 8. a) Schematic representation of the variation of Δf with time in the “increasing” (solid line) and “decreasing” (dashed line) conditions of experiment 4. b) Difference between the mean number of streams heard in the decreasing and increasing conditions of experiment 4. Error bars show +/- one standard error. The right-most and middle bars show data for the neglect and control subjects with the full 6-s sequences shown in part a) of the Fig. The left-most bar shows data for the control

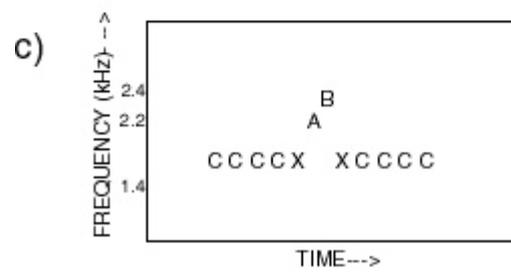
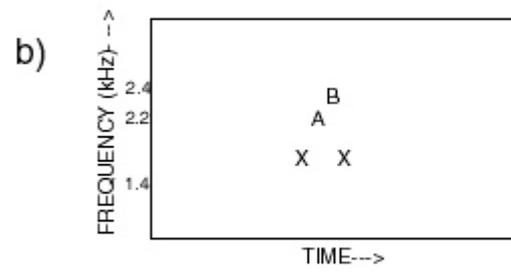
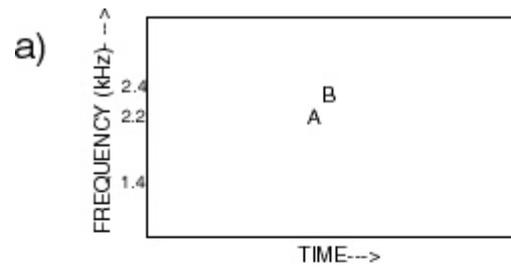
subjects in the condition where the sequences stopped after 3 s (i.e.. at the point where the lines in part a cross). When describing subject groups, the abbreviations R+ and R- are used to describe those with and without right-hemisphere damage, and N+ and N- those with and without neglect.

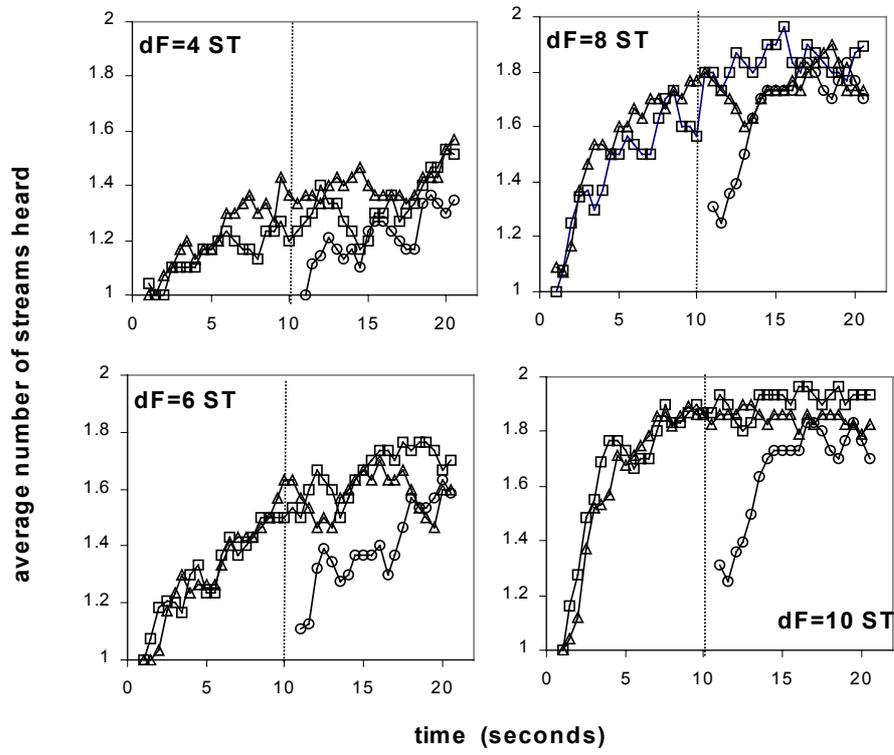
“One stream”



“Two streams”

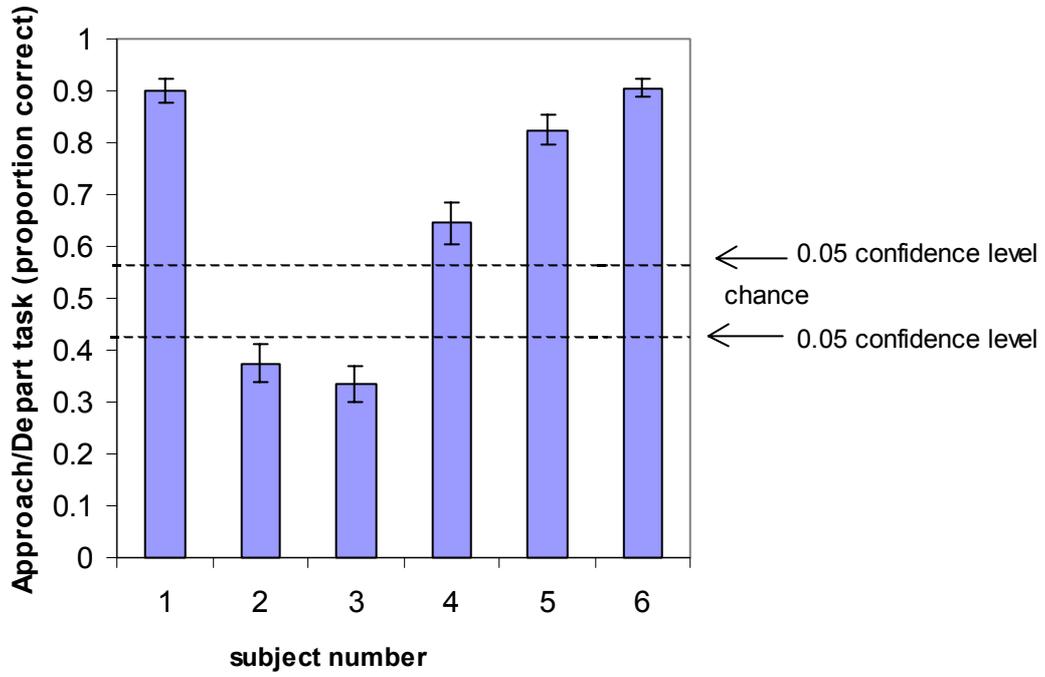


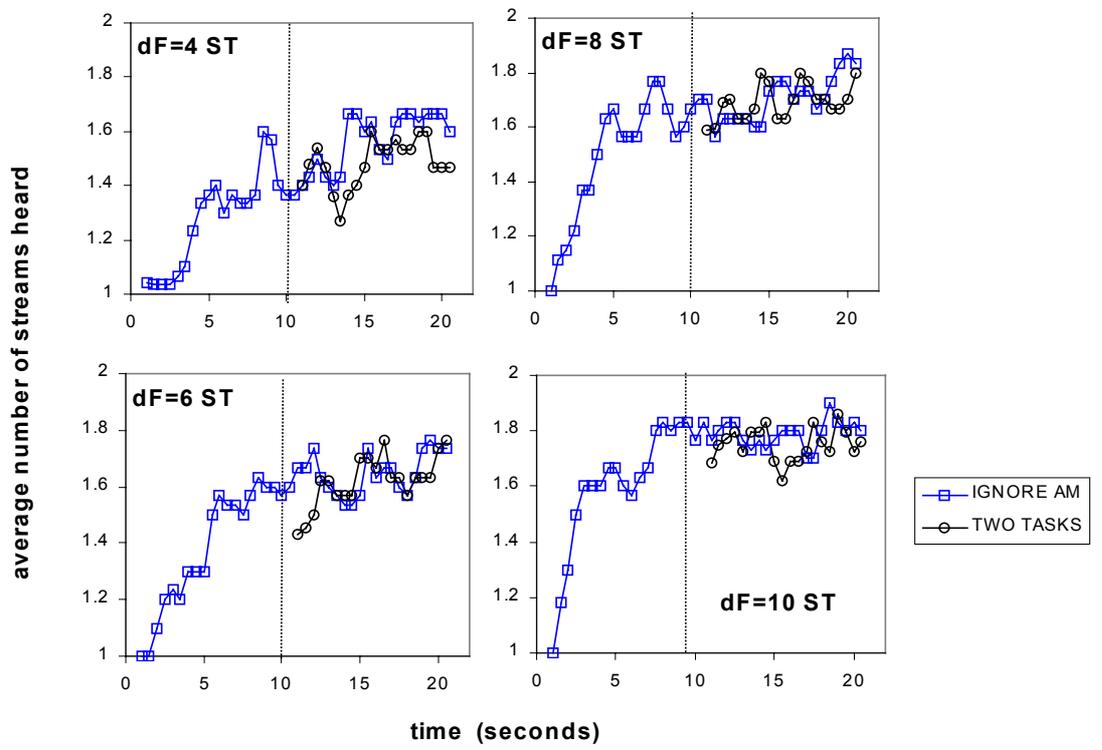




Carlyon et al. Fig. 3

Performance on Distractor Task





Carlyon et al. Fig. 5

