Neglect Between but Not Within Auditory Objects

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Abstract

■ Unilateral neglect is frequently characterized by the presence of extinction, which is a lack of awareness to contralesional visual stimuli in the presence of those further towards the ipsilesional side. It has been established that this visual extinction can be reduced if the stimuli are grouped together into a single object. However, attention between and within auditory objects has never before been studied. We demonstrate for the first time that unilateral neglect—hitherto thought primarily to be a disorder of visuospatial processing—involves a specific deficit in allocating attention between auditory objects separated only in time and not in space. Importantly, this deficit is restricted to comparisons between sounds: the patients' ability to make within-sound comparisons is similar to that of controls. These differences cannot be explained in terms of different time spans over which comparisons must be made. The results suggest unilateral neglect is linked to—if not actually determined by—a reduction in attentional capacity in both the visual and auditory domains, and across the dimensions of both space and time. The findings have potential clinical applications. ■

INTRODUCTION

Our senses are constantly bombarded with information, only a fraction of which is actually relevant to us. It would be wasteful and impossible for us to process this mass of information to any degree, and so it is vital that we select the relevant parts.

In the study of visual selective attention, one of the key findings of recent years has been that we do not just focus attention to particular areas in space, but that we pay attention to particular objects. For example, Duncan (1984) showed that in normal subjects there is a greater cost in attending to multiple features of different objects than in attending to multiple features of the same object. This finding has been confirmed by subsequent studies in many elegant ways (e.g., further psychophysical studies: Behrmann, Zemel, & Mozer, 1998; Driver & Bayliss, 1989; EEG recording: Valdes-Sosa, Bobes, Rodriguez, & Pinilla, 1998; fMRI: Fink, Dolan, Halligan, Marshall, & Frith, 1997). There has also been substantial progress in identifying potential neural mechanisms by which the coding of object formation might occur (Lee & Blake, 1999). It is thought that neurons in the visual system fire in synchrony to indicate that they represent a common object.

The important role of object formation is also illustrated by the strong effect it can have on performance in those with attentional deficits. For example, consider the disorder of unilateral neglect. In the classic demonstration of neglect, patients miss stimuli on the contralesional side when there is an ipsilesional stimulus competing for attention. This is thought to be the result of a pathological bias in attention towards the ipsilesional side. Recently, it has been shown that the extinction of a contralesional stimulus by an ipsilesional one can be much reduced if they are arranged such that the two perceptually group into a single object (Mattingley, Davis, & Driver, 1997; Ward, Goodrich, & Driver, 1994). Again, this suggests that competition for attention acts between objects formed by preattentive grouping.

Humphreys (1998) also made a distinction of between-object and within-object representations. He found a double dissociation between two patient groups with different lesion locations. One group was impaired at reading longer words, but not at counting the number of letters; another group was impaired at counting but not at reading. On the basis of this, Humphreys argued for the between-object and within-object representations, which are mediated by the dorsal and ventral pathways, respectively.

In these accounts, objects at different locations in space compete for attention, with impaired performance in neglect patients resulting from a lateralized attentional bias. Here, we present evidence for a quite different deficit, in attending to multiple sounds, even when they are presented sequentially and close to midline. No such deficit is observed in either age-matched controls or nonneglect patients with right frontal lesions. Our results show that: (i) object formation plays an important role in auditory attention; (ii) competition between (auditory) objects can occur even when only one object is presented at a time; and (iii) this competition occurs even when the sounds are all in the same spatial location. We argue that our results suggest a reframing of neglect in terms of a general, supramodal deficit in attending to multiple objects, and that this more general nonlateralized deficit in attending to multiple objects might in part underlie the lateralized effects observed in previous experiments, such as the role of grouping in extinction described above. The proposed reframing of neglect has important implications for future research and approaches to rehabilitation. We present three pairs of experiments, which show that patients are impaired at making between but not within sound comparisons, and rule out a number of alternative explanations.

RESULTS

Between-Sound Comparisons are Impaired

We measured how well listeners can discriminate the spatial location of sounds in two different ways. In one task, we presented a single sound on each trial, and asked for a simple "left/right" judgement. By examining performance in the transition between the region where they always say "left" and the region where they always say "right," we obtained a measure of ability to discriminate different spatial locations. If a subject were extremely good at spatial discrimination, we would expect a steep transition between left side and right side judgements: if they were bad, we would expect a shallow transition. In a second task, we presented three sounds, one of which (either the second or the third) was in a different location to the other two. We varied the size of this difference, and calculated another measure of their spatial discrimination. If the limitation on performance were sensory, these two methods should yield similar results.

Table 1a shows details of the neglect patients tested. We assessed visual neglect using the line-bisection and star-cancellation components of the Behavioural Inattention Test. All were a considerable time post-CVA (mean 27, range 24–34 months). Four patients participated in Experiments 1a (the one-interval task) and 1b (the three-interval task). Three were below the standard cut-off score on both visual neglect tasks; one was outside the normal range only on the star-cancellation task. We presented the sounds using headphones and manipulated their perceived location. One way to alter the perceived location of a sound is to introduce a difference between the sound intensity levels at the two ears (interaural level difference, ILD). However, this has a problem in that in order to alter the ILD, the level must be changed in one or other of the ears and an

Table 1. Details on Subjects

Patient code	*Experiments done*	*Age*	*Lesion location (all right hemisphere only)*	*Line bisection (maximum: 9)*	*Star cancellation (maximum: 52)*
(a) Details of neglect patients participating in the experiments					
SKZ	1	56	no scan available	9	36[a]
FBR	1, 2	73	parietal	3[a]	49
RTT	1, 3	75	parietal (temporal, frontal)	5[a]	47[a]
CGQ	1, 2, 3	58	frontal (parietal, temporal)	6[a]	28[a]
NFX	2	74	no scan available	7[a]	42[a]
HR	2	75	frontal	5[a]	47[a]
KHN	2	53	parietal	5[a]	51
DDN	2, 3	73	no scan available	0[a]	6[a]
KD	2, 3	75	internal capsule	0[a]	–
(b) Right hemisphere lesion nonneglect control group					
NGB	2b	63	frontal	9	52
RR	2b	51	frontal	9	52
TFI	2b	45	frontal	9	52

In the line-bisection task, the normal range is 8–9, and in the star-cancellation task, the normal range is 50–52.

[a]This result is outside the normal range.

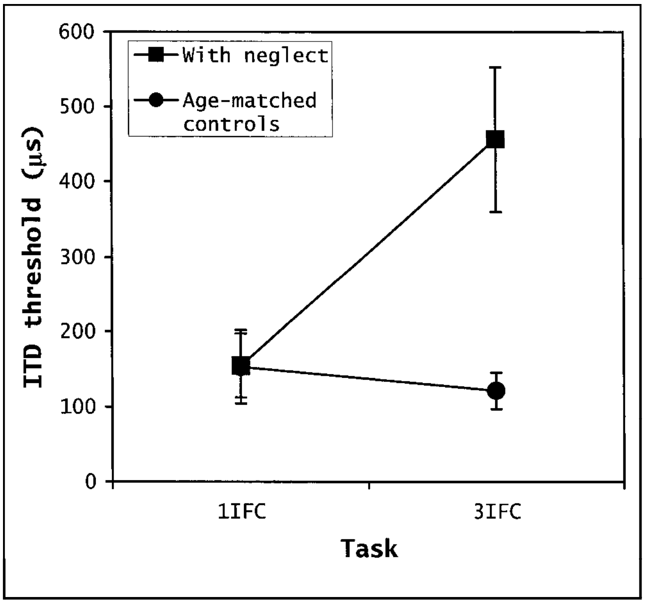

Figure 1. The ITD discrimination thresholds of neglect patients and age-matched controls as derived from one-interval (Experiment 1a) and three-interval (Experiment 1b) forced-choice tasks. Mean values with one *SEM* are shown.

additional cue is introduced—instead of comparing perceived locations, it might be possible for a listener to perform the test on the basis of the level a single ear. To avoid the use of such a cue, we did not use level differences, but an alternative manipulation. We introduced slight differences in the relative timing of the signal to the two ears (introducing an interaural time difference, ITD). The delay between the ears required to shift the perceived location is very small (of the order of tens of microseconds). Although this will have resulted in minute changes in the timing between successive sounds presented to each ear, these within-ear differences would have been several orders of magnitude below threshold.

Figure 1 shows the thresholds measured using the one- and three-interval tasks. As described above, the discrimination thresholds were obtained from the one-interval task by analysis of the slope of the function relating the proportion of "left" judgements to the ITD. In the three-interval task, thresholds were obtained by adjusting the size of the difference between the sounds until performance reached a specified level. In the single-interval task (Experiment 1a), neglect patients and age-matched controls were found to have similar ITD discrimination thresholds ($F(1,9) = .000$, $p = .983$). However, in the three-interval task (Experiment 1b) the patients performed much worse than the control group ($F(1,9) = 16.6$, $p < .005$). In a repeated-measures analysis on the combined data from Experiments 1a and 1b, there was a significant main effect of group ($F(1,9) = 13.2$, $p < .01$) and a task by group interaction ($F(1,9) = 7.58$, $p < .025$). Relative to the controls, the neglect patients were severely impaired on the three-interval task. It seems that the patients might be impaired at making comparisons between different sounds. However, it is also possible that the spatial distribution or close temporal proximity of the sounds led to the performance decrement. To study these possibilities, we designed a second pair of experiments.

An Effect of Shifting Location or an Attentional Blink?

One possible explanation for the results of Experiment 1 is that the neglect patients had difficulty in shifting their attentional focus in space. This would have selectively impaired their performance on the multisound task. To test this, our second pair of experiments compared performance on two tasks in which all sounds were presented identically to both ears, giving them the same perceived location (close to the center of the head in control subjects). The stimuli are shown in Figure 2. In the first, one-interval task (Experiment 2a), subjects were required to say whether a pure tone was steady, or had a frequency modulation (FM, "warble") imposed on it. In the second, two-interval task (Experiment 2b), they were required to indicate which of two sequentially presented tones had the higher pitch. If the results of Experiment 1 were due to a spatially specific deficit,

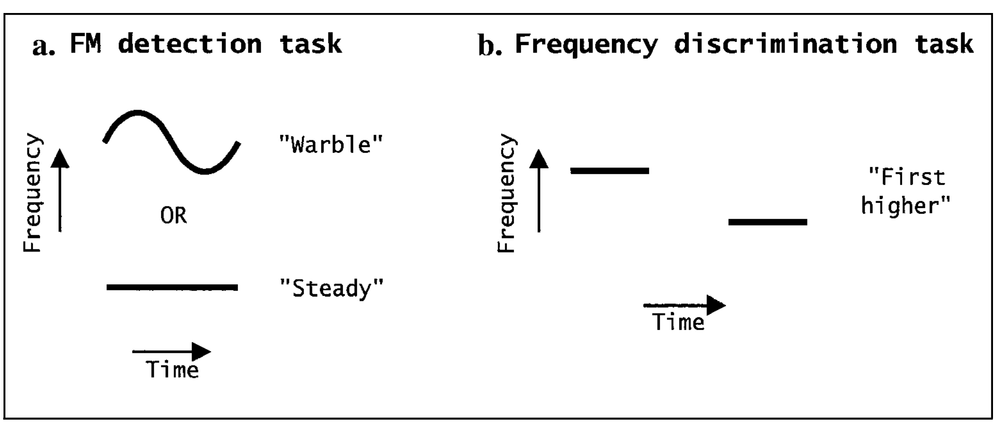

Figure 2. In Experiment 2a (left), listeners had to determine whether a single sound was frequency modulated or not. In Experiment 2b (right), listeners heard two tones, and had to determine whether the first or the second was higher in pitch.

then neglect patients and controls should show similar performance to each other on both tasks. If, however, there is a deficit in making comparisons between but not within sounds, irrespective of their spatial locations, then the neglect patients should be impaired on the two-interval task (Experiment 2b) but not at the one-interval task (Experiment 2a).

A second possibility is that the deficit observed in Experiment 1b was due to the extended "attentional blink" that has been observed (using visual stimuli) in neglect patients. When normal subjects make a speeded response to a target, they often miss a second target coming shortly afterwards (Raymond, Shapiro, & Arnell, 1992). Husain, Shapiro, Martin, and Kennard (1997) demonstrated that this "attentional blink," measured with visual stimuli, is many times longer in patients with neglect. Because the time courses of auditory and visual attentional blinks are similar, at least in normal subjects, this suggests that neglect might lead to extended auditory attentional blink. This, in turn, might explain neglect patients' poor performance in the multiple-sound tasks (Experiments 1b and 2b), because later sounds might fall in the attentional blink of the earlier ones, hindering comparisons between them. We tested this idea by varying the time course of the stimuli. In one task, subjects were again required to make a comparison between sounds. We used two, rather than three sounds, so that if an attentional blink was important, it is clear what was affecting what. We chose a range of intervals that span the shortest and longest intervals used by Husain et al. If performance is limited by an effect similar to the attentional blink, then the deficit observed in neglect patients should decrease at very long interstimulus intervals. Two of the patient group had previously participated in Experiment 1.

Figure 3 shows the just-detectable FM detection thresholds, as measured using a single-interval task (Experiment 2a). It can be seen that although some of the patients were found to have higher thresholds than the normals, there was considerable overlap between the two groups, and the difference was nonsignificant ($F(1,14) = 1.70$). Figure 4 shows performance in the two-interval pitch discrimination task (Experiment 2b) as a function of ISI. The neglect patients (filled squares) were severely impaired relative to the age-matched controls. To confirm that this impairment was not the result of the slight differences in frequency-resolving ability, we calculated the average performance of the four neglect patients with the best FM thresholds in the same range as the age-matched controls. This is shown in the curve marked with open squares on Figure 4. Performance is slightly better than for the complete group, but they are still highly impaired. To test the significance of this finding statistically, we entered the FM detection thresholds measured in Experiment 2a as covariates into the analysis of Experiment 2b. Group remained a highly significant factor ($F(1,9) = 18.6$, $p <$

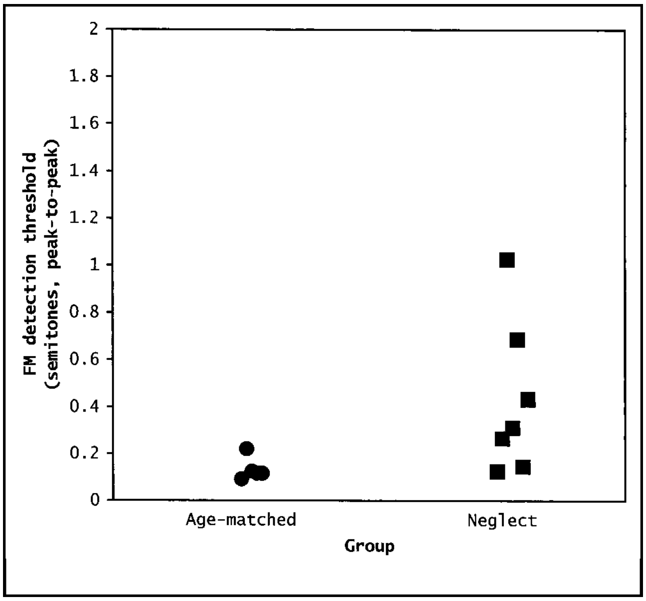

Figure 3. FM detection thresholds in neglect patients and age-matched controls (Experiment 2a).

$.002$) even though the between subjects covariate of FM-resolving ability was found to have some effect ($F(1,9) = 5.37$, $p < .05$). The within-subjects effect of the gap between the sounds also just reached significance ($F(3,27) = 3.51$, $p < .05$), as did the gap by group interaction ($F(3,27) = 3.66, p < .05$), and the gap by FM interaction ($F(3,27) = 4.69, p < .01$). Despite this variance with gap, a post hoc test revealed a significant difference between the patient- and age-matched control groups even for the condition with the smallest difference (250 msec: $t(9) = 2.43, p < .05$). To test the specificity of the problem to neglect patients, we tested three nonneglect controls with right frontal lesions. The results are shown on Figure 4 by the filled triangles. Their performance was very similar to that of the age-matched controls. Figure 5 shows individual performance, collapsed over the different time intervals. Note that all of the neglect patients performed worse than any of the controls.

The main effect of gap and the gap by group interaction appear to be due to slightly better performance by the patient group at the smallest interval between the sounds. It is possible that we would also have seen this in the control group if they were not performing at ceiling. Alternatively, the patients may be slightly less impaired in this condition. One candidate explanation for this is that because of the small interval between the two sounds, they were in some way starting to perceptually group together into a single object. This might overcome a between-sound deficit, making comparisons easier and improve performance.

A Sensory Memory Deficit?

Our results are not what we would expect from an attentional blink like that found by Husain et al.

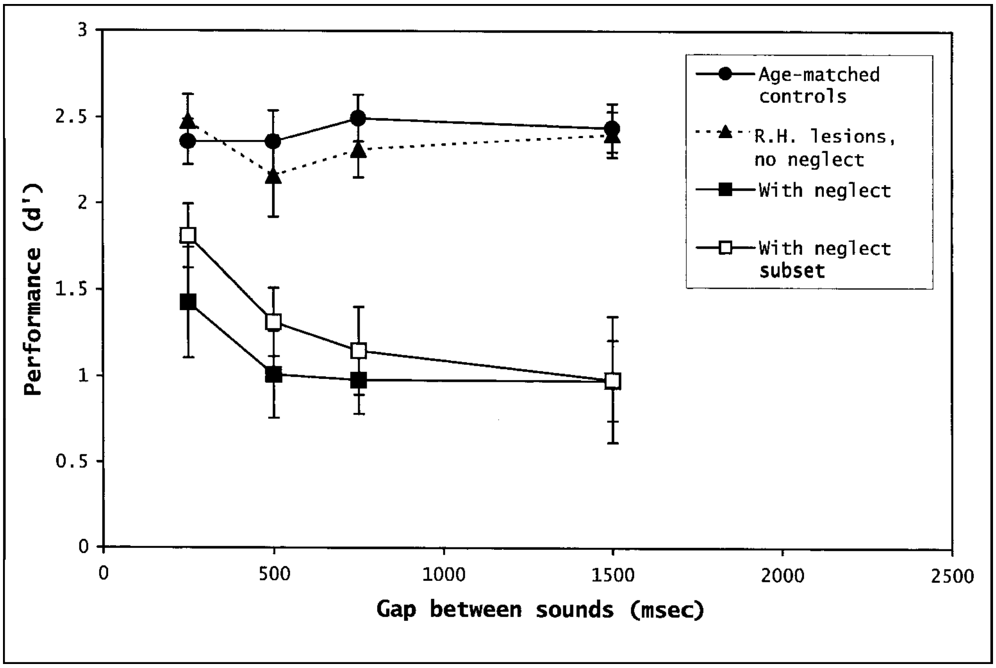

Figure 4. Frequency discrimination thresholds as a function of the intersound interval for three groups (Experiment 2b). Mean values with one *SEM* are shown.

(1997). In their task, Husain et al. found a dip in the performance that was maximal for short gaps between tasks, and that returned to normal after around 1 sec. In our data, performance did not get better as the gap between the stimuli increased, and was impaired even with a 1.5-sec gap.

Another candidate explanation for the results of Experiment 2 might be that the problem is one with sensory memory. Could the results be explained if the memory of sounds decays very quickly, preventing comparisons over longer intervals? This seems unlikely, for the following reasons. Normal subjects will have compared the pitch of the sound at points separated by half a modulation cycle (e.g., at its most extreme frequency deviations—Figure 6; Hartmann & Klein, 1981). At a rate of 2 Hz, these peaks are 250 msec apart. As many of the patients performed well within the normal range, they must also have made comparisons over this time-scale. In Experiment 2b, the minimum gap length used was 250 msec, and these patients were severely impaired even at this gap length. Differences in comparison interval do not seem able to explain the results.

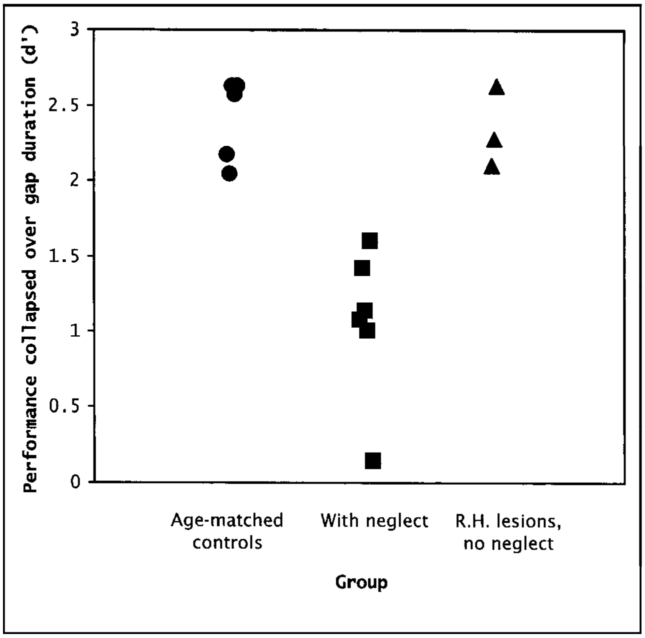

Figure 5. Individual performance of the three groups on the frequency discrimination task (Experiment 2b).

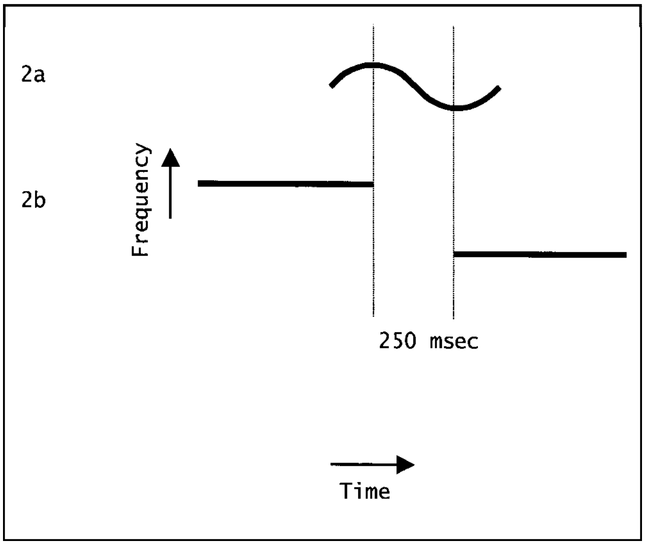

Figure 6. Comparison intervals in Experiments 2a and 2b.

To further examine the importance of memory we tested two patients on FM detection at a slower modulation rate, with sounds of twice the duration. If comparisons could only be made over a limited period, a substantial worsening in performance would be expected. The FM thresholds of the two patients at the two rates were not significantly different (DDM: $F(1,2)$ = .66, CGQ: $F(1,2)$ = 1.50). To look at these data in finer detail, we derived the underlying psychometric functions, which are shown in Figure 7. It can be seen that there was little difference between performance at the two rates. Performance of these two subjects on the two-interval frequency discrimination task (Experiment 2b) with an interval of 250 msec is also shown on Figure 7 (filled triangle). It should also be noted that for similar performance (d') to that produced by a 1.5 semitone difference between sounds, patients needed only a 0.2 semitone FM swing. Making comparisons over longer periods of time seems to have little effect on performance. Rather, it is making comparisons between objects at which the patients have a deficit. Further, Experiment 2a demonstrates that when comparisons within sounds are required, performance is not significantly impaired.

It should be noted that what we have ruled out is a deficit in *sensory* memory. We feel that at higher levels, the boundaries between "attention" and "memory" are not perfectly defined. For example, a deficit in attending to multiple sounds might be reframed as a problem "maintaining multiple objects in working memory." Although we have used the framework of attention to describe the deficit (as we feel this is the most direct), it is not our intention to suggest that it could not be presented in other ways.

Judgement of Temporal Order

Another potential explanation might be that the neglect patients have a problem judging the temporal order of sounds. There is evidence that judgement of temporal order deteriorates with age (Parkin, Walter, & Hunking, 1995). It is possible that a general impairment of functioning in the neglect patients affects their order judgement. To test this, we ran a further experiment with two conditions. Both conditions involved FM detection, but only the second required judgement of temporal order. The first was similar to the single-interval FM-detection task of Experiment 2a. In the other condition, we presented three sounds to subjects. One of the three (either the second or the third) was an FM tone (a "warble"), while the other two were pure tones. Subjects were asked to name the interval containing the warble—either "second" or "third."

Figure 8 shows the results. Controls and patients performed very similarly on both the one- and three-interval FM-detection tasks, indicating that they can identify the temporal order of the sounds. There are several possible explanations for the absence of any impairment in Experiment 3b, in contrast to the strong effects observed in Experiments 1b (three-interval location discrimination) and 2b (two-interval pitch discrimination). One possibility is that in Experiment 3b, the patients were only attending to a single interval (either the second or the third). For example, if no warble is heard in the second interval, the patient can determine that it must be in the third interval. While this explanation remains a possibility, it is surprising that they performed this somewhat sophisticated strategy without error and that none reported or gave hints that they were using such a

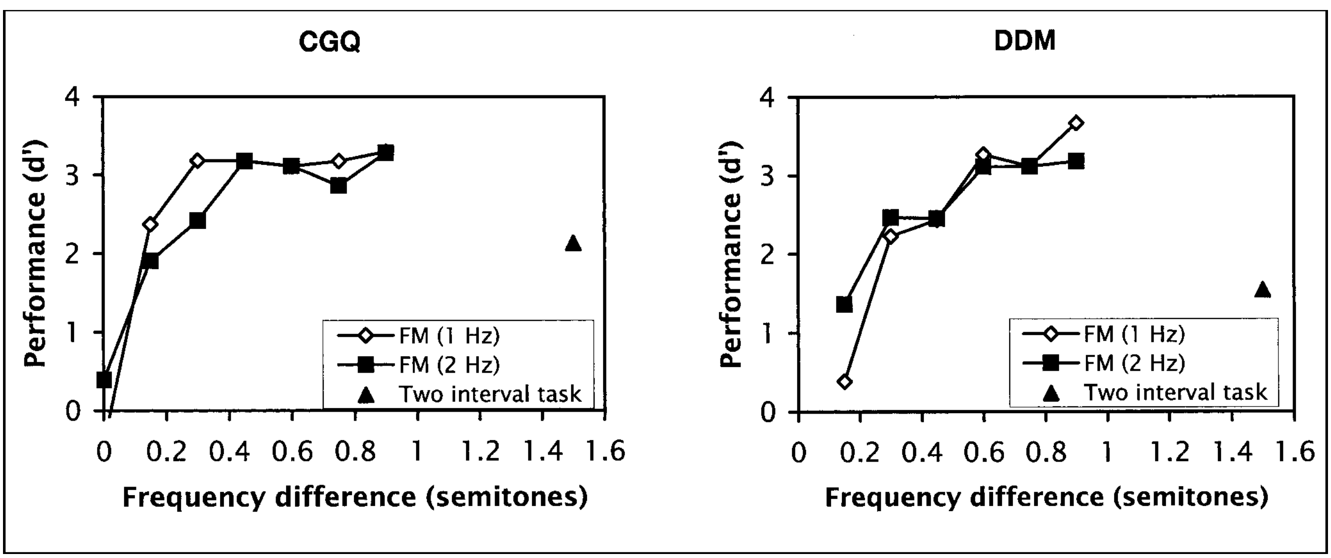

Figure 7. Psychometric functions for two neglect patients on FM detection task (Experiment 2a) at two different rates, and the two-tone frequency discrimination task (Experiment 2b) with a separation of 250 msec.

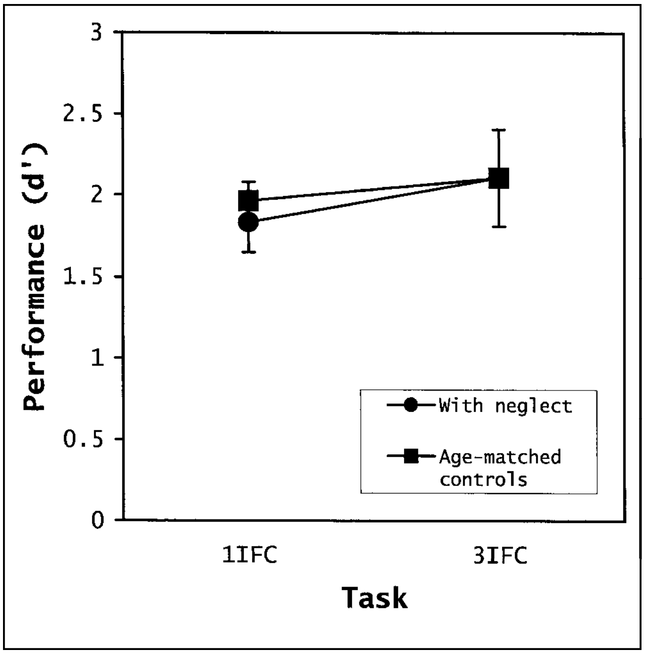

Figure 8. Performance on the one- and three-interval FM-detection tasks (Experiment 3) for neglect and control group. Mean values with one *SEM* are shown.

strategy. However, even if patients did this, the results still demonstrate that one of the later sounds is available for selection and full analysis. The explanation that we prefer is that in this experiment, patients did not have to perform any comparisons between sounds. Each sound can be analyzed individually, and a decision made about whether it is a target or not. It is possible that the FM feature "pops out" in a similar way to additional features in visual search tasks (Edgworth, Robertson, & MacMillan, 1998). Indeed, recent evidence of this in normal listeners has been presented (Cusack & Carlyon, 2000).

DISCUSSION

Task Difficulty?

One trivial explanation for our data might be that the multiinterval tasks are more complicated, and hence any general impairment reduces performance in them. There are three arguments against this. First, two- and three-interval tasks are usually considered easier than single-interval tasks, and to reflect purely sensory processes (Hanna, 1992). Second, the control group with frontal lesions, who might be expected to have the most difficulty with complex tasks, performed near-perfectly on the two-interval task, and in a very similar way to the age-matched controls. Third, on a three-interval task in Experiment 3b the same neglect patients performed no worse than age-matched controls (and in fact, slightly better). Might it then be argued that the three-interval FM detection task in Experiment 3b involved easier discriminations, and so the proposed additional difficulty due to the multiinterval task was hidden? This seems unlikely, as for the age-matched controls, d' values were actually lower in Experiment 3b than in Experiment 2b (two-interval pitch discrimination), suggesting the discrimination was more difficult. Given these three arguments, it seems that our results are unlikely to be the result of a general impairment in task performance, but rather some specific problem with comparisons between sounds.

Is the Deficit Supramodal?

There is good evidence that the auditory deficit we identify is linked to *visual* deficits. In the patient group, which was selected on the basis of visual tests, all were impaired on our *auditory* tasks. From inspection of Table 1, it is apparent that the patients' lesions were distributed over many sites. Several of the patients had significant parietal lesions, but others had only frontal or subcortical lesions. It is well established that lesions in many areas can lead to neglect, which is taken as evidence of the presence of an interconnected attentional network (Mesulam, 1981). That the deficits we observe were found in all of these patients, but not in any of a control group without neglect, suggests that the deficit is intimately connected with the disruption of the attentional systems that leads to neglect. It further follows that the co-occurrence of these auditory deficits with neglect is not just due to lesions to adjacent anatomical areas: the lesion locations in the neglect subjects are too diverse for this to be the case. There is more direct evidence to suggest that analogues of the deficit we report here might occur in vision. Duncan (1998) describes how, when neglect patients are presented with displays of many letters, they show bilateral impairments in the number they can recall: this is exactly what would be expected from a nonlateralized deficit in attending to multiple objects.

When relating visual extinction and our sequential deficit, we should also remember that visual neglect also has a temporal component. There is good evidence that neglect patients do not perceive the onsets of simultaneously presented visual stimuli on the left and right as simultaneous. Rorden, Mattingley, Karnath, and Driver (1997) showed that a stimulus on the left must lead one on the right by several hundred milliseconds to be perceived as synchronous. Such "prior entry" effects have also been observed in primate studies in which frontal and medial eye fields were ablated (Schiller & Chou, 1998).

Might Nonlateralized Deficits Underlie Neglect?

The importance of understanding nonlateralized deficits is underlined by some recent findings. It has been shown using an auditory task that over a time course of tens of seconds, neglect patients show a deficit in nonspatial sustained attention (Robertson et al., 1997). Indeed, its presence is a more reliable indicator of neglect than are some standard tests. It was theoretically predicted by Posner (1993) on the basis of reduced arousal. Additionally, some lateralized aspects of neglect can be reduced by a nonlateralized manipulation that increases arousal (Robertson, Mattingley, Rorden, & Driver, 1998), providing strong support for the idea that nonlateralized problems may in part underlie it.

Dorsal and Ventral Auditory Streams?

The idea of separate dorsal and ventral visual-processing streams is now well established (Milner & Goodale, 1995). As discussed in the Introduction, Humphreys (1998) has argued that a difference between these streams is a focus on between- and within-object processing. Although analogous dorsal and ventral pathways in hearing have been proposed (Pinek, Duhamel, Cavé, & Brouchon, 1989), little evidence for them has been accrued. We show that our group of neglect patients has a specific deficit in auditory between-object comparisons while within-object comparisons are entirely unimpaired. This is consistent with the presence of separate representations for the two types of information. Identification of patients with deficits making comparisons within but not between sounds would complete the dissociation and imply that dual auditory pathways exist. Our experiments also demonstrate that the perceptual grouping into objects (sounds) is important in auditory attention. Further experiments, perhaps with normal subjects, might further elucidate how this affects attention to sounds.

Clinical Applications

There are two ways in which our findings might have immediate clinical application. As can be seen in Figure 4, the effects observed are very robust. This, the simplicity of the stimuli and task in the two-interval pitch discrimination task (Experiment 2b), and the speed with which data can be gathered (40 trials in 4 min), give the task good potential for development into a clinical test to aid diagnosis of neglect. As an auditory task, it would have the benefit of unambiguously differentiating low-level visual problems (e.g., hemianopia) from neglect. The frequency discrimination task has the advantage that it will not be oversensitive to inaccurate reproduction (e.g., cassette tape) or small hearing losses in one or both of the ears. Secondly, if the lateralized aspects of neglect are the result of a nonlateralized deficit, it has potential implications for approaches to rehabilitation. Rather than (or in addition to) advising practice at laterally shifting attention towards the neglected side, one might promote recovery by training patients to attend to multiple objects separated in time. Further research in these directions has the potential for promising advances in the diagnosis and treatment of neglect.

METHOD

Experiment 1

We conducted the experiments using a portable computer with a WavJammer soundcard (distortion < – 70 dB) and Sennheiser HD-414 headphones at a sample rate of 22,050 Hz. All sounds were 500 msec long, and presented at 60 dB SPL. There were negligible timing or level differences between the headphone speakers (< 1 μs, < 0.25 dB). In Experiment 1a, we presented a single narrow-band noise on each trial, while in Experiment 1b, we presented three similar noises (center frequency = 600 Hz, bandwidth = 60 Hz). Lateralization was manipulated by delaying the noise to one ear slightly (adding an ITD). In Experiment 1a, on each trial, listeners heard a single sound and then verbally indicated its lateralization ("left" or "right"). Two randomly interleaved one-up one-down adaptive staircases were used to converge upon the perceived center. We used initial ITDs of 210 μs (in one staircase, the right led and in the other one, left) and 20-μs steps. In all adaptive procedures, a run terminated after 12 turn points, and the average of turn points 6–12 used as a measure. We gave one run as a practice block, then two for the main data. Ten patients were tested in pilot work for Experiment 1a. Six had perceived centers within the normal range (±150 μs), while two had shifts explicable by asymmetric hearing loss. These data are presented elsewhere (Cusack, Carlyon, & Robertson, 2000), and not discussed in detail here. Four of the patients with central ITD values in the normal range were chosen at random for further analysis and later participation in Experiment 1b.

We derived discrimination thresholds from the data in Experiment 1a by fitting a probit curve to the underlying psychometric functions, and then finding the difference between the 62 and 38 percent points on the functions. This measure, extracted from a one-interval task, should give the same value as the three-interval procedure (Macmillan & Creelman, 1991). In Experiment 1b, identical sounds were used as in Experiment 1a, but three were presented, spaced by 500 msec. On each trial, two sounds were presented at one location (ITD of $x/2$ μs) and one (either the second or the third) on the opposite side (ITD of $-x/2$ μs). The subject had to identify whether the second or the third sound was the "odd man out." The sign of x was randomly chosen for each trial, so that there might have been two sounds on the left and one on the right, or vice-versa. Its magnitude was adjusted using a two-up one-down adaptive procedure. An initial value of 300 μs and step size of 20 μs were used. If anything, the final thresholds for the patients are likely to be an underestimate, as adaptive procedures are unreliable if performance begins at a poor level (i.e., the adaptive parameter is below the threshold). This was the case, as the final staircase value was greater than the initial value for all of the patients.

Experiment 2

In Experiment 2a, we presented a single sound (center frequency 600 Hz) that was either a pure tone or changed in frequency in a sinusoidal manner (FM). The FM had a rate of 2 Hz. In the later 1-Hz control condition, the sounds were similar, but 1-sec long and modulated at the lower rate. We asked for a response of either "steady" or "warble." A two-up one-down adaptive procedure was used to find FM thresholds. We used an initial FM depth of 1 semitone peak-to-peak and a step size of 0.05 semitones. To derive psychometric functions, the trials were allocated to 0.1 semitone-wide bins and d' values calculated for each bin. In Experiment 2b, on each trial, listeners were presented with two pure tones. The tones had a fixed frequency difference (1.5 semitones), with either the first or the second randomly chosen to be the higher tone, and were separated by 250, 500, 750 or 1,500 msec. Listeners were asked which tone was higher. The center frequency of the two sounds was randomly chosen from the range 400–800 Hz to prevent listeners performing the task by listening to a single sound. As practice, 16 trials were given, and repeated if requested. The main data collection comprised 32 trials for each of four time intervals.

Experiment 3

Experiment 3 comprised two conditions. Both involved the detection of changes in frequency within a sound. One condition used the same procedure as Experiment 2a, but in constant stimulus form. To reduce ceiling or floor effects, we used a fixed FM depth, equal to that listener's FM threshold as measured in Experiment 2a. In the other condition, we presented three sounds. Two were pure tones and one, either the second or the third, was an FM tone. We asked which interval contained the FM tone ("second" or "third"). Again, the FM depth was fixed to that listener's threshold from Experiment 2a. There were two blocks of 32 trials for each condition, given in counterbalanced ABBA order. As practice, we preceded the first block of each condition by a block comprising 32 trials at a clearly salient (1 semitone peak-to-peak) FM depth.

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