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Effect of luminance on successiveness discrimination in the absence of the corpus callosum

Bettina Forster[a,*], Paul M. Corballis[b], Michael C. Corballis[c]

[a]*University of Verona, Human Physiology Section, Department of Neurological and Visual Science, Strada La Grazie 8, 37134 Verona, Italy*
[b]*Department of Cognitive Neuroscience, Dartmouth College, Hanover, NH, USA*
[c]*Research Centre for Cognitive Neuroscience, Department of Psychology, University of Auckland, Auckland, New Zealand*

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Abstract

Three split-brained subjects, one with full forebrain commissurotomy and two with callosotomy, were impaired at judging whether pairs of lights in opposite visual fields were successive or simultaneous. This impairment did not vary with luminance when the lights were grey against a dark background, but was more pronounced when the lights were equiluminant with a yellow background. All three subjects were also better able to discriminate succession from simultaneity when the lights were both in the left visual field than when they were both in the right. A fourth subject with callosal agenesis was only slightly impaired relative to normal subjects, who were virtually errorless. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Ramachandran et al. [27] have reported evidence that perception of apparent motion, induced by pairs of lights presented in succession on either side of the vertical midline, is surprisingly little impaired in people who have undergone complete forebrain commissurotomy. One of the subjects, L.B., identified both the presence and direction of succession across the midline with 100% accuracy, while another, A.A., also scored significantly above chance. Moreover, the upper threshold of apparent motion across the midline, where the perception of motion gives way to the perception of simple succession, was approximately the same in L.B. and A.A. as in normal subjects. Another commissurotomised subject, N.G., was highly accurate at discriminating leftward from rightward succession, but judged all simultaneous pairs of lights to be moving. Ramachandran et al. suggested that apparent motion across the midline in the split brain might be mediated by the so-called second visual system, which bypasses the lateral geniculate and relays through the superior colliculus and pulvinar nucleus; indeed, this system may play a more general role in unifying the visual field in commissurotomised patients [31].

Nevertheless, there are some indications that the detection of succession across the midline may be deficient in split-brained people, and may perhaps be based on inference rather than perception of apparent motion. Gazzaniga [13] found that a callosotomised subject, J.W., was unable to discriminate pairs of lights presented in succession on either side of the midline from a single light presented in one hemifield, suggesting that the perception of succession depends on the set created by the experimental conditions. Naikar and Corballis [25] found, however, that the commissurotomised subject L.B., unlike J.W., was able to distinguish single lights from successive pairs with high accuracy, and they also confirmed that he could accurately discriminate leftward from rightward succession,

* Corresponding author. Tel.: +39-45-8098104; fax: +39-45-580881.
E-mail address: bettinaf@borgorma.univr.it (B. Forster).

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and succession from simultaneity. Nevertheless they also found that L.B.'s detection of successiveness across the midline deteriorated markedly when he was required to make a three-way choice between successive pairs, simultaneous pairs, and single lights.

There are further conditions under which L.B.'s ability to discriminate succession from simultaneity across the midline is markedly impaired. In a study in which the stimulus onset asynchrony (SOA) between the lights was varied from 0 to 150 ms, normal subjects reliably distinguished successiveness from simultaneity when the SOA reached 33 ms, but L.B. did not do so until the SOA reached 150 ms [10]. L.B.'s discrimination was close to normal when the stimuli were presented in the right visual field, supporting evidence for a left-hemispheric specialisation for fine temporal discrimination [26]. Further, Naikar [24] found that, even with an SOA of 167 ms, L.B.'s ability to discriminate successiveness from simultaneity across the midline deteriorated when coloured lights replaced brighter white lights, and suggested that the discrimination may be critically dependent on luminance.

In the present study we examine the influence of luminance on the discrimination of successive from simultaneous pairs of lights in L.B., and in three other subjects with commissural anomalies; these were the callosotomised subject J.W., another subject (V.P.) with nearly complete callosotomy, and a man (R.B.) with congenital absence of the corpus callosum. In Experiment 1, the luminance of the stimuli was systematically varied, and in Experiment 2 the stimuli were grey discs presented against an equiluminant yellow background. If the discrimination of succession from simultaneity depends on the collicular pathway, as suggested by Ramachandran et al., then we would expect the discrimination to be especially impaired under equiluminance, a condition thought to largely restrict processing to the parvocellular visual pathways [21], and therefore to bypass subcortical pathways.

2. Experiment 1: luminance variation

2.1. Subjects

The four critical subjects were L.B., J.W., V.P., and R.B. L.B. is a man who underwent section of the forebrain commissures, including the corpus callosum, anterior commissure, and hippocampal commissure for the relief of intractable epilepsy in 1963. Magnetic resonance (MR) images taken in 1987 confirmed complete section of the corpus callosum [3]. Further information on L.B.'s case history is provided by Bogen and Vogel [4]. L.B. is right handed, and was 45 years old at the time of testing.

J.W. is a man who was 44 years old at the time of testing, and V.P. a woman who was 45 years old. Both underwent two-stage surgical section of the corpus callosum in 1979 for the relief of intractable epilepsy. In both the anterior commissure remains intact, and subsequent MR scans show that she has some sparing of fibres in the rostrum and splenium of the corpus callosum [14].

R.B. is a man who was subjected to MR examination in 1988 at the age of 12 years, after complaining of headaches and visual fatigue. This revealed that he lacks a corpus callosum and that the posterior portions of his lateral ventricles are enlarged. He has no history of epilepsy. Standard neurological examinations and subsequent experiments have revealed few manifestations of hemispheric disconnection except for some lengthening of interhemispheric transfer time as estimated from simple reaction time to lateralised light flashes, and a deficit in coarse stereopsis in central vision [1]. He is left-handed, with a laterality index of -14 on a scale that ranges from -24 to $+24$ [5]. He was 20 years old at the time of testing.

2.2. Stimuli

The stimuli consisted of pairs of grey disks of diameter 0.86° and luminance 64.9, 23.2, 7.8, or 3.1 cd/m^2 presented against a darker grey background (0.5 cd/m^2). Each pair was presented either in the left visual field (LVF), with the two disks centred at 7.5° and 2.5° from central fixation, or bilaterally, with the disks centred at 2.5° to the left and right of fixation, or in the right visual field (RVF), with the disks again centred at 2.5° and 7.5° from fixation. The angular separation between the disks of each pair was therefore 5°. These angular distances for fixation are sufficient to ensure that each disc is projected to the contralateral hemisphere [12].

When a trial was triggered, a small cross appeared in the middle of the screen for 480 ms, and served as a warning signal. This was followed by a blank screen for 17 ms, and then the stimulus sequence began. For successive presentations, one disk appeared for 133 ms, followed by a blank field for 33 ms, followed by the second disk for 133 ms. The SOA was therefore 167 ms. On half the successive trials, the left disk appeared before the right, and on the other half this was reversed. For simultaneous presentations, both disks were presented together for 133 ms. All of the different conditions were randomly ordered within a block of trials.

Within each block of trials, there were four successive and four simultaneous presentations at each luminance in each presentation location (LVF, bilateral, and RVF). The blocks varied somewhat across the subjects. For the control subjects, the disks were displayed at all four luminances (64.9, 23.2, 7.8, and 3.1

cd/m^2), making a total of 96 trials per block. For J.W., V.P., and R.B. the disks were displayed only at the three higher luminances (64.9, 23.2, and 7.8 cd/m^2), making a total of 72 trials per block. L.B. also received blocks at these three luminances, and addition blocks at the two lowest luminances (7.8 and 3.1 cd/m^2).

2.3. Procedure

The subjects were instructed that they would see pairs of lights, and that they should press the N key on the computer keyboard if the lights appeared to be simultaneous and the M key if they appeared to be successive. They were instructed to use the forefinger and middle finger of the same hand to press the keys.

Prior to the experimental trials, all subjects received ten practice trials with each hand. For these trials, the conditions were selected randomly from the conditions making up the experimental trials. The control subjects received four blocks of 96 experimental trials. Half the subjects used the left hand for the first block, the right hand for the second and third blocks, and the left hand for the fourth block. V.P. and J.W. received eight blocks of 72 trials. The assignment of hands over the eight blocks for both subjects was left, right, right, left, left right, right, and left. L.B. and R.B. received four blocks of 72 trials, and the assignment of hands over the blocks for both was right, left, left, and right. L.B. received four further blocks of 48 trials in which the luminances were 7.8 and 3.1 cd/m^2.

2.4. Results

Fig. 1 plots the proportion of "successive" responses to successive and simultaneous pairs for each stimulus location, and luminance. The bottom right panel shows that this task is trivially easy for subjects with

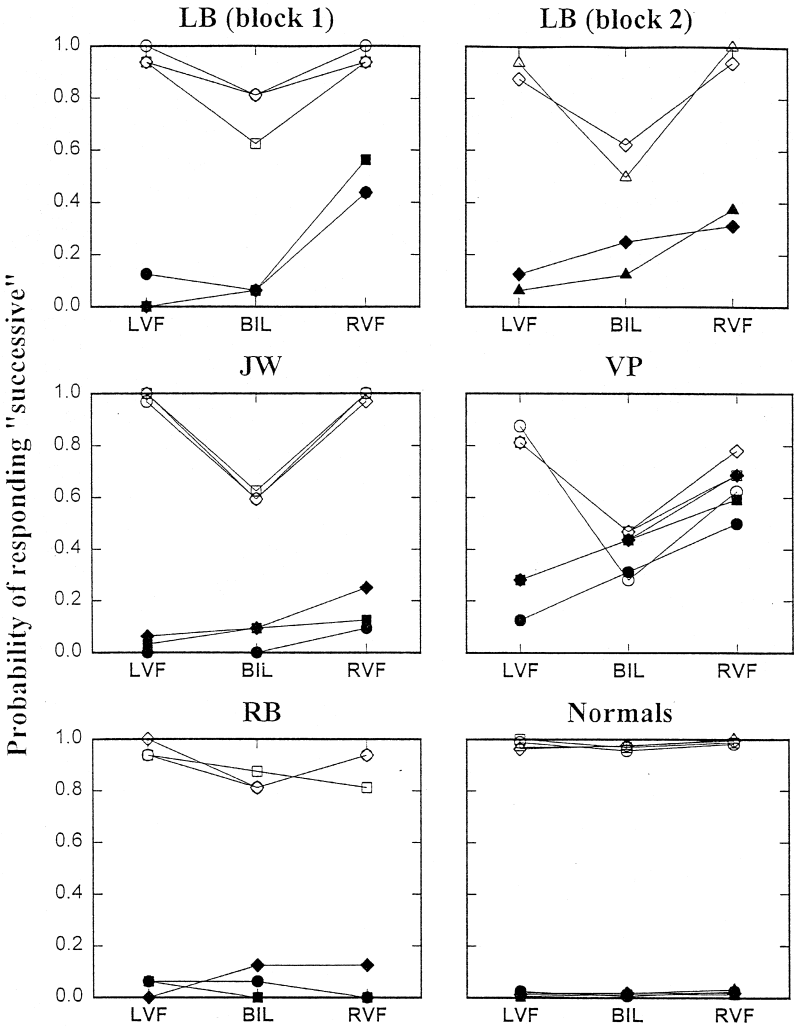

Fig. 1. Probability of responding "successive" at each stimulus location in Experiment 1. Unfilled symbols = successive stimuli, filled symbols = simultaneous stimuli; circles = 64.9 cd/m^2, squares = 23.2 cd/m^2, diamonds = 7.8 cd/m^2, triangles = 3.1 cd/m^2.

Table 1
Values of the fourfold-point correlation N for each split-brained subject, under each condition of luminance in each location, in Experiment 1[a]

Subject	Luminance (cd/m^2)	Location		
		LVF	Bilateral	RVF
L.B. (Series 1)	64.9	0.88***	0.76***	0.63***
	23.2	0.94***	0.59**	0.43*
	7.8	0.94***	0.76***	0.54**
L.B. (Series 2)	7.8	0.75***	0.38*	0.65***
	3.1	0.88***	0.40*	0.67***
J.W.	64.9	0.97***	0.65***	0.82***
	23.2	0.97***	0.55***	0.88***
	7.8	0.94***	0.53***	0.74***
V.P.	64.9	0.75***	−0.03	0.13
	23.2	0.53***	0.03	0.10
	7.8	0.53***	0.03	0.11
R.B.	64.9	0.88***	0.76***	0.94***
	23.2	0.88***	0.88***	0.83***
	7.8	1.00***	0.69***	0.81***

[a] ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.

intact commissures; the control subjects were able to perform the task virtually without error, and the discrimination was not influenced by luminance. The results for the split-brained subjects are shown individually in the remaining panels. As a measure of the subjects' ability to discriminate successive from simultaneous stimuli, the fourfold-point correlation N between stimuli and responses was computed for each luminance at each location, separately for each split-brained subject, and the results are shown in Table 1.

For the split-brained subjects, the data were analysed individually, using multivariate chi-squared analyses to determine the effects on response selection ("successive" vs "simultaneous") of the stimulus type (successive vs simultaneous), stimulus location (LVF vs bilateral vs RVF), hand (left vs right), and luminance, and their interactions [32].

2.4.1. L.B.

L.B.'s response selection as a function of luminance for the three locations is plotted in the top two panels of Fig. 1. In the first series of four blocks (*top left panel*), for which the luminances were 64.9, 23.2, and 7.8 cd/m^2, L.B.'s response selection varied significantly with the stimuli [$\chi^2(1, N = 288) = 139.86$, $p < 0.001$], indicating that, overall, he responded at well above a chance level. There was also a significant main effect of location on response selection [$\chi^2(2, N = 288) = 139.86$, $p < 0.001$], indicating different response biases across the three locations. As Fig. 1 shows, this was largely attributable to a bias to respond "successive" to stimuli in the RVF.

More importantly, there was a significant interaction between stimulus and location [$\chi^2(2, N = 288) = 9.26$, $p < 0.01$], indicating that discrimination accuracy varied across the three locations. Pairwise comparisons showed that accuracy was significantly higher for LVF than for RVF stimulus pairs [$\chi^2(1, N = 192) = 9.65$, $p < 0.001$], but there were no significant differences between LVF and bilateral pairs [$\chi^2(1, N = 192) = 2.50$, N.S.] or between bilateral and RVF pairs [$\chi^2(1, N = 192) = 2.12$, N.S.]. There were no significant main effects or interactions involving hand or luminance.

Analysis of L.B.'s response selection in the second series of blocks (*top right panel* of Fig. 1), in which the luminances were 7.81 and 3.1 cd/m^2, also revealed a highly significant main effect of stimulus [$\chi^2(1, N = 192) = 70.11$, $p < 0.001$], indicating good overall discrimination. There were also significant main effects of hand [$\chi^2(1, N = 192) = 6.75$, $p < 0.01$] and location [$\chi^2(2, N = 192) = 10.17$, $p < 0.01$], and a significant interaction between the two [$\chi^2(1, N = 192) = 6.50$, $p < 0.02$]. Again these effects can be attributed to a strong bias to respond "successive" with RVF presentations, but the bias was more marked with the left hand (0.72) than with the right hand (0.59).

There was again a significant interaction between stimulus and location, indicating that the discrimination varied across locations [$\chi^2(2, N = 192) = 6.17$, $p < 0.02$]. In this case, pairwise comparison showed significantly better discrimination for LVF than for bilateral pairs of stimuli [$\chi^2(1, N = 128) = 6.22$, $p < 0.02$], but there were no significant differences between LVF and RVF [$\chi^2(1, N = 128) = 1.15$, N.S.] or between bilateral and RVF [$\chi^2(1, N = 192) = 2.50$, N.S.] pairs. As Table 1 shows, however, discrimination was worst for bilateral pairs, although significantly above chance under all conditions of location and luminance.

2.4.2. J.W.

J.W.'s response selection as a function of luminance for the three locations are also plotted in Fig. 1 for each luminance (64.9, 23.2, and 7.8 cd/m^2). There were main effects of stimulus [$\chi^2(1, N = 576) = 349.52$, $p < 0.001$], indicating above chance discrimination overall, and of location [$\chi^2(2, N = 576) = 23.80$, $p < 0.001$], indicating variation in response bias across locations. As Fig. 1 shows, this can be attributed to a stronger tendency to response "simultaneous" to bilateral than to either LVF or RVF pairs.

There was a significant interaction between stimulus and location [$\chi^2(2, N = 576) = 17.61$, $p < 0.01$], indicating that discrimination accuracy varied across the three locations. The discrimination was significantly worse for bilateral than for either LVF [$\chi^2(1, N = 384) = 17.08$, $p < 0.001$] or RVF [$\chi^2(1, N = 384) = 8.24$, $p < 0.01$] pairs, but there was no difference between LVF and RVF [$\chi^2(1, N = 384) = 1.51$, N.S.]. Table 1 shows that J.W.'s discrimination was neverthe-

less above chance at each luminance in each location. There were no significant effects or interactions involving hand or luminance.

2.4.3. V.P.

V.P.'s response selection, plotted in Fig. 1 for each luminance (64.9, 23.2, and 7.8 cd/m^2), varied significantly with stimulus [$\chi^2(1, N = 576) = 33.15$, $p < 0.001$], indicating above-chance discrimination overall, and with location [$\chi^2(2, N = 576) = 23.10$, $p < 0.001$], indicating differential response bias across locations. This was attributable in part to a bias to respond "simultaneous" to bilateral pairs, and to respond "successive" to RVF pairs (see Fig. 1).

There was also a significant interaction between stimulus and location [$\chi^2(2, N = 576) = 39.23$, $p < 0.01$]. Pairwise comparisons showed that the discrimination of successive from simultaneous pairs of stimuli was significantly better for LVF than for either bilateral [$\chi^2(1, N = 384) = 34.00$, $p < 0.001$] or RVF [$\chi^2(1, N = 384) = 24.78$, $p < 0.01$] pairs, but there was no difference between bilateral and RVF pairs [$\chi^2(1, N = 384) = 0.85$, N.S.]. Table 1 shows that V.P.'s performance was significantly above chance only in the case of LVF pairs. There were again no significant effects or interactions involving hand or luminance.

2.4.4. R.B.

R.B.'s response selection, again plotted in Fig. 1 for each luminance (64.9, 23.2, and 7.8 cd/m^2), varied significantly only with stimulus [$\chi^2(1, N = 288) = 207.36$, $p < 0.001$], indicating a high level of discrimination under all conditions. Table 1 shows that he was above chance under all conditions of location and luminance.

2.5. Summary

It is clear that all three cases of surgical section of the commissures were impaired in the discrimination of successive from simultaneous pairs when they were presented bilaterally. In the case of J.W., discrimination of bilateral pairs differed significantly from discrimination of both LVF and RVF pairs, and in the case of L.B. (second series) and V.P. it differed significantly from discrimination of LVF pairs. However, only V.P. failed to score significantly above chance with bilateral pairs. These effects did not depend significantly on luminance. The data are in marked contrast to those of the normal subjects, who scored virtually at ceiling under all conditions.

The results for L.B., in particular, are surprising, given that an earlier study showed him to be virtually perfect at discriminating bilateral pairs presented at the highest of the luminances used here, and with the same SOA [25]. Our result suggests that L.B.s poor performance with coloured stimuli, reported by Naikar [24], cannot be attributed simply to the lower luminance of those stimuli. Taken in conjunction with those results, our findings suggest that perception of apparent motion across the midline is dependent on context, and deteriorates when the stimuli vary from trial to trial in either colour or luminance.

An unexpected aspect of the results is that discrimination was better for LVF than for RVF stimuli; this trend was evident in all three subjects with surgical section of the commissures, although it was significant only in the case of L.B. and V.P. This LVF advantage is surprising in view of earlier evidence that L.B., in particular, shows a strong *RVF* advantage in detecting successiveness when the SOAs are very short [8,10]. For the normal subjects, accuracy was too close to ceiling for any difference to be detectable.

The acallosal subject R.B.'s discrimination was clearly above that of the three surgical cases. Nevertheless his performance was somewhat below that of the normal subjects. Indeed he was worse than any of the normals with bilateral and RVF presentations, in line with the general trend shown by the three surgical cases.

3. Experiment 2: equiluminance

In this experiment we sought to further reduce the role of luminance by presenting the lights against an equiluminant background. In general, perception of motion is impaired under conditions of equiluminance (e.g., [2,11,28]), although there are at least some circumstances under which people *can* see the movement of patterns that are defined by colour rather than luminance (e.g., [7,23]). To the extent that the discrimination of successiveness depends on the perception of apparent motion, we might therefore expect it to be impaired within as well as between visual fields under conditions of equiluminance. However, if the discrimination of successiveness across the midline depends on collicular response, then we might expect it to be especially impaired in this case, on the assumption that collicular response is largely abolished under equiluminance.

There is some evidence that this is so. Simple reaction time to flashes of light in split-brained subjects is markedly shorter when pairs of lights are presented, one in each visual field, than when single lights are presented. This is known as the *redundant target effect*, and is paradoxically much more pronounced in split-brained subjects than in normal people [9,29]. However, this effect was largely abolished in split-brained subjects when the stimuli were equiluminant, consistent with the view that the redundant target effect depends on neural summation at the collicular level, and that collicular re-

sponse is at least attenuated, if not eliminated, by equiluminance [9].

Equiluminance was achieved by presenting the stimuli in low-level blue light against a bright yellow background. Against this background, the lights actually appeared to be light grey. This is not only a robust technique for approximating equiluminance, but also effectively eliminates colour-defined borders [6].

3.1. Subjects

The subjects were the same as in Experiment 1.

3.2. Stimuli

The stimuli were the same as those in Experiment 1, except that instead of varying in luminance they were presented under conditions of equiluminance. Equiluminance settings were determined using flicker photometry in an RGB system allowing each of red, green, and blue wavelengths to be varied on a scale from 0 to 63. The background of the VGA screen was set to yellow by choosing maximum settings of 63 for each of red and green, and the 0 setting for blue. A black circle with radius 1° then appeared in the centre of the screen. After 700 ms it was replaced by a flickering disk, also of radius 1°, for 1 s. The disk was generated by adding 30, 35, 40, 40, or 45 units of blue to

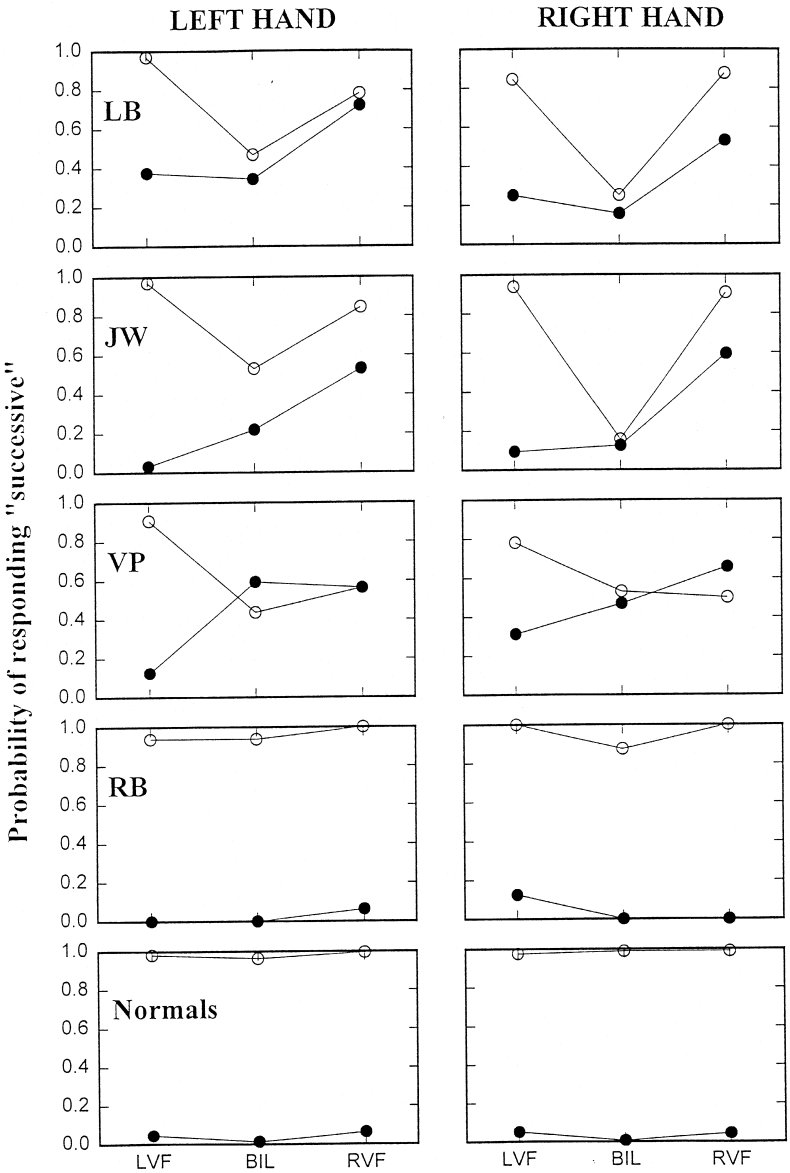

Fig. 2. Probability of responding "successive" at each stimulus location in Experiment 2. Unfilled circles = successive stimuli, filled circles = simultaneous stimuli.

the yellow background, and at the same time subtracting 0, 1, 2, or 3 units of red. The grey disk so generated alternated with the yellow background at 16 on-off cycles per s. There were five blocks of 60 trials, involving all combinations of added blue and subtracted red. The subjects were asked to indicate whether or not the disk appeared to flicker. The settings used for the equiluminance displays were the combinations that minimised the perception of flicker. For the three split-brained subject and the acallosal subject, the disk was seen as continuous (not flickering) when the blue increment was 35 units and the red decrement 3 units. This setting was also most often used for the normal subjects as well.

3.3. Procedure

This experiment was carried out following Experiment 1, so that the subjects had already had experience with the basic task. All subjects were given four blocks of 96 trials, with responding hand counterbalanced as in Experiment 1.

3.4. Results

Fig. 2 plots the proportion of "successive" responses to successive and simultaneous pairs for each stimulus location and hand. The bottom two panels show that this task is again trivially easy for subjects with intact commissures. The results for the split-brained subjects are shown individually in the remaining panels. Fourfold-point correlations, N, were computed between stimuli and responses for each hand at each location, separately for each split-brained subject, and the results are shown in Table 2.

For the split-brained subjects, the data were analysed individually, using multivariate chi-squared analyses in which the classification variables were response selection ("successive" vs "simultaneous"), stimulus (successive vs simultaneous), location (LVF vs bilateral vs RVF), and hand (left vs right).

Table 2
Values of the fourfold-point correlation N for each split-brained subject, computed for each hand at each location, in Experiment 2[a]

Subjects	Left hand Location			Right hand Location		
	LVF	Bilateral	RVF	LVF	Bilateral	RVF
L.B.	0.63***	0.13	0.07	0.60***	0.12	0.38***
J.W.	0.94***	0.33**	0.34**	0.84***	0.04	0.36**
V.P.	0.78***	−0.16	0	0.47***	0.06	−0.16
R.B.	0.94***	0.94***	0.94***	0.88***	0.88***	1.0***

[a] ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.

3.4.1. L.B.

L.B.'s response selection, plotted in the top two panels of Fig. 2, varied significantly with stimulus [$\chi^2(1, N = 384) = 35.35, p < 0.001$], indicating that, overall, he responded at well above a chance level. There were also significant effects of location [$\chi^2(2, N = 288) = 48.99, p < 0.001$], and of hand [$\chi^2(1, N = 288) = 6.05, p < 0.05$]. L.B. showed a bias to respond "simultaneous" to bilateral stimulus pairs and "successive" to RVF pairs (see Fig. 2), and overall he had a stronger overall bias to respond "successive" with the left (0.61) than with the right (0.48) hand.

There was a significant interaction between stimulus and location [$\chi^2(2, N = 384) = 17.05, p < 0.001$], indicating that discrimination accuracy varied across the three locations. Pairwise comparisons showed discrimination accuracy to be significantly worse for bilateral than for LVF stimulus pairs [$\chi^2(1, N = 256) = 15.13, p < 0.001$], and worse for RVF than for LVF pairs [$\chi^2(1, N = 256) = 11.01, p < 0.001$], but there was no significant difference between bilateral and RVF pairs [$\chi^2(1, N = 256) = 0.56$, N.S.]. Although the triple interaction between stimulus, location, and hand was not significant [$\chi^2(2, N = 256) = 1.91$, N.S.], Table 2 shows that discrimination was significantly above chance in the RVF when L.B. used his right hand but not when he used his left hand. The discrimination failed to rise significantly above chance with bilateral presentation for either hand, but was significantly above chance with LVF presentation for both hands.

3.4.2. J.W.

Response selection varied significantly with stimulus [$\chi^2(1, N = 384) = 97.65, p < 0.001$], and location [$\chi^2(2, N = 384) = 54.53, p < 0.001$]. There was also a significant interactions between hand and location [$\chi^2(2, N = 384) = 6.52, p < 0.05$]. Fig. 2 shows that there was a strong bias to respond "simultaneous" to bilateral stimulus pairs, especially with the right hand, and a bias to respond "successive" with RVF pairs.

There was a significant interaction between stimulus and location [$\chi^2(2, N = 384) = 37.15, p < 0.001$]. Pairwise comparisons showed that discrimination was significantly better when the stimulus pairs were in the LVF than when they were either bilateral [$\chi^2(1, N = 256) = 34.98, p < 0.001$] or in the RVF [$\chi^2(1, N = 256) = 18.55, p < 0.001$], but there was no difference between bilateral and RVF pairs [$\chi^2(1, N = 256) = 1.27$, N.S.].

3.4.3. V.P.

There was a significant main effect of stimulus [$\chi^2(1, N = 384) = 10.72, p < 0.01$], a significant interaction between stimulus and location [$\chi^2(2, N = 384) = 40.61, p < 0.001$], and a marginal interaction between stimulus, location, and hand [$\chi^2(2, N = 384) = 4.80, p <$

0.10]. Pairwise comparisons among the three locations were carried out separately for each hand. For the left hand, discrimination of LVF stimulus pairs was significantly better than that for either bilateral [$\chi^2(1, N = 256) = 28.15$, $p < 0.001$] or RVF [$\chi^2(1, N = 256) = 19.65$, $p < 0.001$] pairs, but the difference between bilateral and RVF pairs was not significant [$\chi^2(1, N = 256) = 0.79$, N.S.]. For the left hand, too, discrimination of LVF pairs was significantly better for LVF [$\chi^2(1, N = 256) = 5.29$, $p < 0.05$] and bilateral [$\chi^2(1, N = 256) = 12.70$, $p < 0.01$] pairs, but there was again no significant difference between LVF and bilateral pairs [$\chi^2(1, N = 256) = 1.54$, N.S.]. Table 1 shows that V.P.'s performance was significantly above chance only in the case of LVF pairs.

3.4.4. R.B.

For R.B., the only significant effect was that of stimulus [$\chi^2(1, N = 384) = 165.04$, $p < 0.001$], indicating that overall discrimination was well above chance.

3.5. Summary

The results are similar to those of Experiment 1, although the effects are sharper. Among the three cases of surgical section of the commissures, discrimination of bilateral stimuli rose above chance only in the case of J.W.'s performance with the left hand. Discrimination of RVF stimuli was somewhat better, rising above chance for J.W. and for L.B.'s right-hand performance. Discrimination of LVF stimuli was above chance for all three subjects, regardless of hand. The poor performance with bilateral presentation might well be attributed to equiluminance, which should, in principle at least, have eliminated or at least attenuated the afferent response of the midbrain visual system.

The acallosal subject R.B. was again well above chance in all conditions, although still somewhat below normal.

4. Discussion

It is clear from the experiments reported here that the discrimination of simultaneity from succession across the vertical midline following commissurotomy is more fragile than the earlier studies of Ramachandran et al. [27] and Naikar and Corballis [25] might suggest. In Naikar's [24] study, L.B.'s ability to discriminate the direction of successive pairs of coloured lights was markedly poorer when the lights were presented bilaterally than when they were presented unilaterally. Experiment 1 suggests that lowered luminance per se does not account for Naikar's result; the discrimination decrement with bilateral presentation was independent of luminance, and evident even when the luminance matched that of the study by Naikar and Corballis. The difference is probably not due to differences in spatiotemporal parameters: With an SOA of 167 ms, the timing of the stimuli in this study was the same as that in Naikar and Corballis's study, and the spatial separation was 5°, which lies between the two spatial separations (2 and 7°) used by Naikar and Corballis. It appears that the context created by varying luminance was sufficient to raise the threshold for detecting succession across the midline.

Bilateral performance in the split-brained subjects was if anything even worse when the stimuli were equiluminant. If the subcortical pathways were largely unresponsive to equiluminant stimuli, then this would also have negated any subcortically mediated switch in attention from across the visual fields with successive presentation. If the discrimination of successiveness depends on this switch of attention, as Naikar [24] suggests, then this might explain why the discrimination generally dropped to chance. This is not to deny the possibility of some residual subcortical responsiveness to equiluminance, perhaps mediated by collicular-pulvinar interactions [30], and this may explain why J.W. was able to achieve above-chance discrimination with his left hand. It is clear that the normal subjects were as accurate in Experiment 2 as in Experiment 1, consistent with previous evidence that equiluminance does not prevent the discrimination of successiveness in normals [7,15,23].

It is also possible, however, that at least part of the difficulty with bilateral presentation was due to the incompetence of the left hemisphere, since all three split-brained were much more accurate for RVF than for LVF pairs.[1] This was an unexpected result. V.P., in particular, was never able to achieve above-chance discrimination of either RVF or bilateral pairs, but she performed relatively well with LVF pairs, implying that the difficulty was not due to failure to understand the instructions. J.W. was generally more accurate with RVF pairs than with bilateral ones, as was L.B. in Series 2 of Experiment 1 and in Experiment 2, suggesting that bilateral presentation presented extra difficulties. The RVF deficit in L.B. was in marked contrast to the RVF *advantage* that L.B. showed in previous studies involving discrimination of rapid succession from simultaneity [8,10]. This is consistent with

[1] A more recent study with L.B. has suggested a deterioration in his left-hemisphere function [9], evident not only in his test performance but also in his general demeanour. In the present study, however, we did not note the slurring of speech and right-sided weakness that was later to become evident, and even if some left-hemispheric pathology may explain L.B.'s LVF advantage in this study, it does not of course explain the LVF advantage shown by the other split-brained subjects.

evidence reviewed by Ivry and Robertson [17] that the left hemisphere is the more attuned to high temporal (as well as spatial) frequencies, and the right hemisphere to low frequencies. It is perhaps worth noting that, in Experiment 2 but not in Experiment 1, the split-brained subjects tended to respond more accurately when the responding hand was ipsilateral to the input than when it was contralateral to it, suggesting that processing may have been confined more exclusively to the receiving hemisphere under equiluminance.

The acallosal subject R.B. showed neither the bilateral deficit nor the RVF deficit shown by the three commissurotomised subjects, confirming previous evidence that the functional disconnections observed in subjects with callosotomy or full forebrain commissurotomy are not evident, or are much attenuated, in callosal agenesis, probably because of compensatory mechanisms operating from early childhood [18,20]. Lassonde et al. [19] have nevertheless shown there are limits to the compensation observed in callosal agenesis; in particular, these subjects may be impaired on visual and tactile tasks involving midline fusion, and that "the deficits observed in acallosal subjects may be of the same amplitude as those observed in [surgically] split-brain patients" (p. 1002). Discrimination of successiveness across the midline clearly does not fall into this category of tasks, at least for R.B., although his performance was somewhat below the essentially perfect discrimination shown by the normal subjects.

It is also of interest that callosotomy appears to result in impaired performance even when the stimuli were presented unilaterally — relative to the performance of normals, this impairment was evident in both visual fields, although it was more marked in the RVF than in the LVF. This may relate to evidence that the optokinetic reflex is impaired in split-brained subjects if only the nasal or temporal hemiretinas are stimulated [22], implying a callosal contribution that proceeds via area MT to subcortical nuclei [16]. While stimulation was never restricted to a single hemiretina in the present study, the absence of a callosal input may have nevertheless introduced some fragility to the percept. More generally, Lassonde et al. [19] have noted that both acallosals and those with surgical section of the corpus callosum may show deficits in a number of tasks involving unilateral presentation, including binocular depth perception and sound localisation, suggesting a nonspecific, possibly supramodal influence of callosal disconnection on cortical activation.

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