



Cortical and subcortical contributions to the representation of temporal information

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Received 2 October 2002; received in revised form 19 December 2002; accepted 26 March 2003

Abstract

Converging evidence suggests that temporal representations of brief durations are derived subcortically. We tested split-brain patient JW in order to investigate whether these representations project bilaterally or unilaterally to cortex. Using visual stimuli to signal time intervals, JW was asked to compare the duration of a pair of standard stimuli that were presented bilaterally with a comparison stimulus that was presented to either the left or right visual field. Assuming the hand of response is controlled by the contralateral cerebral hemisphere, a hand by visual field interaction was predicted if the representation of stimulus duration was restricted to the cerebral hemisphere receiving the lateralized stimulus. However, we failed to observe this interaction for two different ranges of stimulus durations, both in the hundred (Experiment 2) to hundreds (Experiment 1) of milliseconds range. Instead, there was a consistent right hemisphere advantage in task performance. When the task then required a discrimination based on the physical size of the stimuli rather than their duration, an interaction between response hand and visual field was obtained (Experiment 3). Taken together, these results suggest that (1) even though the comparison stimulus was presented unilaterally, the representation of its duration was available to both cerebral hemispheres, and (2) a right hemisphere advantage in psychophysical tasks requiring the comparison of successive stimuli is observed for temporal and non-temporal judgments.

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Keywords: Time perception; Cerebellum; Basal ganglia; Split-brain; Callosotomy; Corpus callosum; Hemispheric asymmetry

1. Introduction

The accurate encoding of temporal information is integral to normal human function. Precisely-timed behaviors depend on the ability to both encode and reproduce temporal intervals that maintain a high degree of fidelity to objectively-measured time. By most cognitive accounts, the representation of brief time intervals is assumed to reflect the existence of an internal “clock”, a representational capacity in which neural events bear some isomorphic relationship to objectively-measured time. Although there remains much to be learned about the neural instantiation of an internal clock, it has been hypothesized that subcortical mechanisms play a critical role (Braitenberg, 1967; Ivry, 1996; Matell & Meck, 2000). In the following paper we explore this hypothesis in a series of interval discrimination experiments conducted with a split-brain patient.

Evidence that a putative internal clock may be linked to subcortical mechanisms has come from a variety of sources.

This work has focused on the cerebellum and basal ganglia, two structures that have extensive reciprocal connections with the cerebral cortex. Lesions in the cerebellum in humans are associated with deficits in the temporal control of movements (Franz, Ivry, & Helmuth, 1996; Ivry & Keele, 1989; Ivry, Keele, & Diener, 1988; Timmann, Watts, & Hore, 2000), impaired performance on duration discrimination tasks (Ivry, 1996), and a reduced ability to judge stimulus velocity (Grill, Hallett, Marcus, & McShane, 1994; Ivry & Diener, 1991; Nawrot & Rizzo, 1995). Converging data in support of the cerebellar timing hypothesis has been reported in the neuroimaging literature, where studies using positron emission tomography (PET) have found increases in cerebellar blood flow during visual-based duration judgments (Maquet et al., 1996), auditory-based duration judgments (Jueptner et al., 1995), and somatosensory-based velocity judgments (Jueptner, Flerch, Weiller, Mueller, & Diener, 1996).

The relationship of the cerebellum and prefrontal cortex on perceptual timing tasks has been explored in recent studies that directly compared the performance of patients with lesions of either of these structures (Casini & Ivry, 1999;

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Mangels, Ivry, & Shimizu, 1998). The results have suggested that, whereas lesions of the cerebellum directly affect the ability to encode temporal information, prefrontal lesions interfere with maintaining and monitoring these representations in working memory. Thus, damage to either brain region may disrupt performance on duration discrimination tasks, but the reasons for the impairments may be distinct.

The basal ganglia have also been tied to the operation of an internal clock. Similar to the cerebellum, basal ganglia activation is consistently observed in imaging studies requiring temporal discriminations (Jueptner et al., 1995; Rao, Mayer, & Harrington, 2001). Psychopharmacological studies point to the involvement of the dopaminergic nigrostriatal pathway. Rats treated with dopamine agonists behave as if perceived time is shorter than objective time while the opposite is observed following treatment with dopamine antagonists (for a review, see (Meck, 1996)). Disorders of dopaminergic systems in humans lead to behavioral changes that parallel the animal data. For example, patients with schizophrenia, a disorder associated with increased dopamine levels, perceive subjective time as quicker than objective time (Wahl & Sieg, 1980). Conversely, patients with decreased levels of dopamine resulting from Parkinson's disease have been found to have a perception of time that passes more slowly than objective time (Malapani et al., 1998; Pastor, Artieda, Jahanshahi, & Obeso, 1992). In short, dopamine levels in the nigrostriatal pathway have been hypothesized to modulate the speed of an internal clock.

Although both the cerebellum and basal ganglia have been tied to the formation of temporal representations, studies using dopaminergic manipulations have tended to use temporal intervals that span a much greater range (e.g. 10–40 s) than the intervals used in cerebellar patient studies (e.g. 100 ms–1 s). Whether similar mechanisms apply to the representation of shorter and longer intervals remains a subject of debate. Some reports have shown that patients with Parkinson's disease are impaired on duration discrimination tasks with intervals ranging around 500 ms (Harrington, Haaland, & Hermanowicz, 1998), while others have reported that these patients perform comparable to age-matched controls (Ivry & Keele, 1989). One hypothesis is that, whereas the nigrostriatal pathway may modulate the subjective experience of the passage of time for intervals in the seconds range, the cerebellum may be essential for the representation of intervals in the tens to hundreds of milliseconds (Ivry, 1996). Further, the two systems may be complementary, with the time-limited cerebellar representations linked to a frontal-striatal system when the task requires the representation of longer intervals, conditions that will engage processes associated with sustained attention and working memory (see (Mangels & Ivry, 2001)).

Given the assumption that temporal representations are derived subcortically, there remain a number of unresolved issues that concern how these representations interact with cortical processes. For example, are temporal representations lateralized and if so, does such lateralization persist between

cortical and subcortical levels of processing? To begin addressing these questions, we studied the performance of a split-brain patient in a visual-based interval discrimination task.

1.1. *The split-brain model*

Surgical sectioning of the forebrain commissures eliminates the ability of the two cerebral hemispheres to directly transfer information derived from a unilaterally-presented stimulus (Sperry, Gazzaniga, & Bogen, 1969; Gazzaniga, Bogen, & Sperry, 1962). As a result, these patients are generally impaired on tasks that require integrating information between the two hemispheres. In vision the effect is revealed by presenting a task-relevant stimulus lateral to fixation, thereby limiting afferent projection from the geniculostriate pathway into only the contralateral cerebral hemisphere. Since direct transcallosal (or interhemispheric) pathways are abolished, information reaching the ipsilateral hemisphere will be indirect, either involving cortico-subcortico-cortico pathways, or an initial non-geniculate projection to the ipsilateral hemisphere. Performance is then compared between trials in which the responses are made with the hand ipsilateral to the stimulus (i.e. when the stimulus was presented to the hemisphere making the response) and trials in which the responses are made with the hand contralateral to the stimulus (i.e. when the stimulus was presented to the hemisphere not making the response). Assuming that the motor system retains this contralateral segregation in the split-brain (Franz, Eliassen, Ivry, & Gazzaniga, 1996), a visual field by hand of response interaction is predicted under conditions where the inability to transfer information callosally disrupts task-related processing (see (Gazzaniga, 1995)). Our goal was thus to determine whether or not a visual field by hand of response interaction would be found in a split-brain patient performing an interval discrimination task.

1.2. *Interval discrimination tasks*

In the canonical interval discrimination task, participants are presented with two intervals of time, each demarcated by visual, auditory, or somatosensory stimuli. The first interval is typically referred to as the “standard”, and its duration is fixed for the entire block of trials. The second interval is referred to as the “comparison”, and the duration of this interval varies from trial to trial. The participant's task on each trial is to judge whether the comparison duration was shorter or longer than the standard duration. While several different models have been proposed to account for performance on interval discrimination tasks (Malapani et al., 1998; Zakay & Block, 1996), they share the assumption that the representation of elapsed time for the comparison interval is compared with a memory trace associated with the standard interval. Adapting this paradigm for split-brain patients, we used the design shown in Fig. 1. Two lines, one on each side of fixation, were presented for a fixed duration, referred to as the

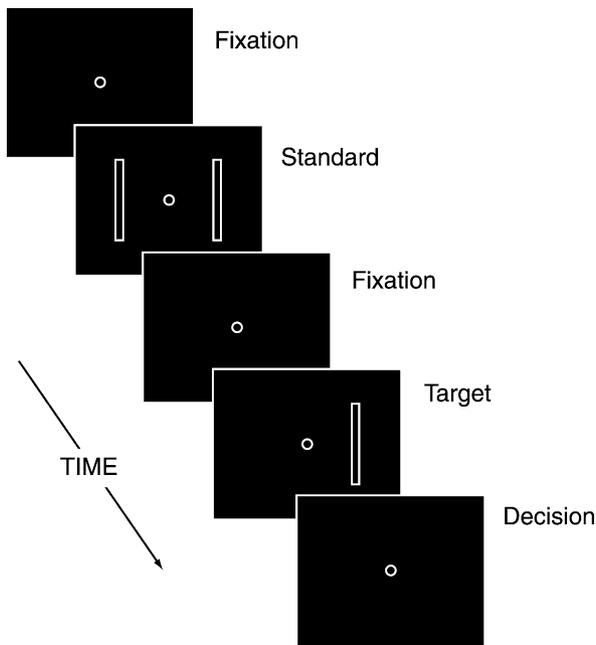


Fig. 1. Display used in Experiment 1. Shown is a trial with the target interval defined by a bar in the right visual field. The duration of the standard interval remains constant on every trial, while the duration of the target interval is systematically varied to be either shorter or longer in duration than the standard. The decision made on every trial was whether the target duration was shorter or longer than the standard duration.

standard interval. In this manner both cerebral hemispheres would have direct knowledge of the standard interval duration. Following a brief delay, a second bar was then presented in either the left or right visual field location, with the side selected randomly. The duration of the second bar signaled the comparison interval. The patient then responded with one hand, indicating whether the comparison interval was shorter or longer in duration than the standard interval. The visual field of the comparison was varied within trial blocks, and the hand of response was varied between trial blocks. In question was whether there would be a difference in response performance as a function of whether the comparison interval was presented in the visual field ipsilateral versus contralateral to the hand of response.

1.3. Predictions

As shown in Fig. 2, there were two competing hypotheses regarding task performance by a split-brain patient. If the temporal representation of a visually-lateralized stimulus remains lateralized in cortex, performance should be better when the visual field of the comparison interval is congruent with the hand of response. That is, there should be an interaction between stimulus visual field and response hand (Fig. 2a). Alternatively, temporal representations of lateralized visual inputs might be accessible bilaterally. For example, subcortical representations might be accessible to both cerebral hemispheres. This could occur if the output from

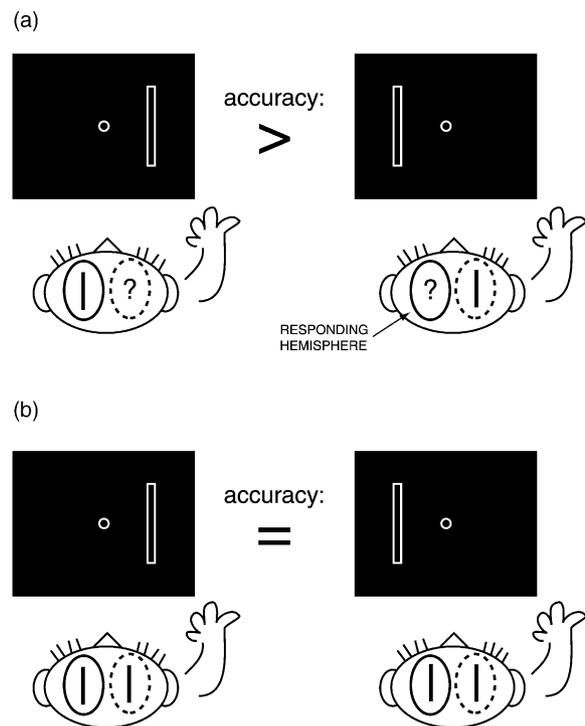


Fig. 2. Two competing hypothesis regarding temporal representations in cortex. Each display shows the visual field to which the target interval is presented. In all instances the right hand is making the response. In question is whether the lateral presentation of the target interval leads to a lateral or bilateral representation of that interval in cortex. (a) Temporal representations may be lateralized. In this case only the hemisphere directly stimulated by the target interval has a representation of the interval. This predicts that performance accuracy will be greater when the hand of response is ipsilateral to the visual field of the target (left), relative to when the hand of response is contralateral to the target (right). (b) Temporal representations may be bilateral. In this case both hemispheres receive the target interval representation independent of the visual field in which it is presented. This predicts performance accuracy will not vary as a function of the visual field in which the target interval is presented.

lateralized subcortical representations was projected bilaterally or if the input to subcortical structures was bilateral. Under either situation, no interaction would be expected between response hand and stimulus visual field (Fig. 2b).

As an initial effort to understand cortical-subcortical interactions on temporal processing tasks, we assessed the merits of these competing predictions in a case study with a callosotomy patient.

2. Experiment 1

In Experiment 1, we tested the split-brain patient JW on a two-alternative, forced-choice duration discrimination task. On each trial, two visual events were presented in succession (see Fig. 1) The first event consisted of two bars, one presented in the left visual field and the other presented at a symmetric location in the right visual field. The bars were displayed for a fixed duration, referred to as the standard

interval. The second event consisted of a single bar, presented in either the left or right visual field. The duration of this event, the comparison interval, was either shorter or longer than the standard interval. An adaptive psychophysical procedure was used to determine the duration of the comparison interval at which JW was correct on 75% of the trials and to estimate the duration judged to be equivalent to that of the standard, the point of subjective equality (PSE). The former measure provides an estimate of temporal acuity; the latter an estimate of response bias. In addition to varying the visual field of the comparison interval (within trial blocks), we also manipulated the hand used to make the responses (between trial blocks). Importantly, by using a within-block manipulation of the side of the comparison interval, the participant should not shift attention to one side or another in advance of this stimulus.

2.1. Method

2.1.1. Participants

Primary testing involved a single participant, patient JW, a 49-year-old right-handed male who was paid for his participation. JW first presented epileptic seizures at age 19. At 25 he had a two-stage callosotomy operation, with the posterior portion sectioned in the first surgery and the anterior portion sectioned in the second surgery. Complete callosal sectioning has been confirmed via MRI and CT anatomical scanning. His post-surgery IQ measured via the WAIS-R was 95. For a more detailed description of this patient, see (Gazzaniga, Nass, Reeves, & Roberts, 1984). Four neurologically-normal males were also tested. Participants 1 (53 years old) and 2 (47) were both age- and education-matched relative to JW, and were paid for volunteering; participants 3 and 4 were authors TCH (38) and RBI (45), respectively. All were right-handed.

2.1.2. Stimuli and procedure

The stimuli were presented on a VGA monitor located approximately 57 cm from the participant, controlled by a 386-based microcomputer. All of the stimuli were white, presented on a black background. Each trial began with the presentation of a small circle (diameter of 0.8°) at the center of the monitor. 1000 ms after the onset of the fixation marker, two vertically-oriented bars were displayed. Each bar was 4.3° tall and 0.3° wide, and were centered approximately 6° to the left and right of fixation (see Fig. 1). The bars were presented for 40 rasters of the 70 Hz monitor, or 571 ms. This duration constituted the standard interval. 1100 ms after the offset of the bilateral bars a single bar of the same size and orientation was presented in one of the two locations of the standard bars. The duration of this bar—the comparison interval—was varied from trial to trial. Following the offset of the comparison stimulus, participants were required to press a button with their thumb if the comparison interval was shorter than the standard interval or press a button with their index finger if the comparison interval was longer

than the standard. The hand used to make these responses was varied between trial blocks. Following the response, the screen was blanked for 800 ms until the reappearance of the fixation marker indicated the onset of the next trial. Participants were instructed to maintain fixation throughout each block of trials.

The parameter estimation by sequential testing (PEST) method was used to determine the perceived duration of the comparison stimulus (Lieberman & Pentland, 1982; Pentland, 1980). This is an adaptive procedure in which each response is used to make a new estimate of temporal acuity based on a “difference threshold.” In brief, the procedure assumes that the participant’s judgments are described by a logistic function in which the probability of responding “longer” will increase with the duration of the comparison interval. Separate estimates are made for thresholds at which the participant correctly responds “shorter” and “longer” on 75% of the trials, respectively. Within this context, the difference threshold is defined as the difference between the “shorter” and the “longer” thresholds. As a consequence, the smaller the difference threshold, the greater the temporal acuity.

At the beginning of each trial block the logistic function is initialized with an experimenter-defined difference threshold, set in the current experiment at seven raster sweeps (or approximately 100 ms). Following each response, a new estimate is made based on the participant’s performance. For example, if the current trial is estimating the short threshold and the participant judges the comparison to be longer, then the logistic function is assumed to be flatter, yielding a new threshold estimate that is shorter. The procedure is repeated for 30 trials per threshold, or a total of 60 trials, with the trials used for the two threshold estimates interleaved in a random manner. The step size used was 1 raster cycle (or approximately 14 ms). The PEST procedure is both efficient and robust. Stable estimates are obtained with 25–30 trials per threshold and these estimates are minimally affected by the initialization values.

At the end of the block, the difference threshold divided by two was used as the measure of temporal acuity. This value corresponds to one standard deviation of the logistic function, and is what is reported in the Tables and statistics below as the “difference threshold”. The midpoint between the two threshold values provided the measure of the PSE, the value at which the participant was equally likely to respond “shorter” or “longer”. Participants were provided with feedback at the end of each block concerning their acuity.

Ten practice trials were included at the start of each block. A fixed set of comparison interval durations was used for these trials: for each of the four PESTs (2 visual fields \times 2 thresholds, shorter and longer), the difference between the standard and comparison was 357 ms. This large difference was included so that the experimenter could ensure that participants understood the task instructions. The second practice trial for each PEST involved a difference of 214 ms. For

the last two practice trials, one for each visual field, the standard and comparison were of equal duration. There was no pause between the practice and test trials and participants were not aware of the transition between these phases. A brief rest was provided after the 60 test trials.

JW completed six test sessions, with each session consisting of two blocks, one in which he responded with the left hand and one block in which he responded with the right hand. Control participants performed one session each. The response board was always oriented so that the thumb and index finger formed a line perpendicular to the plane of the video screen with the thumb closer to the body. This configuration was used to minimize compatibility effects that might arise between the side of the stimulus and the side of the response keys. The order of the two blocks within each session was counterbalanced between sessions (for JW) and between subjects (for control participants).

To confirm that JW could maintain fixation during the task, eye movements were monitored during the sixth session via scleral reflectance using an IView eye tracking system (SensoMotoric Instruments Inc., Needham, MA). The eye-tracking data confirmed what we observed informally during the other sessions, namely that JW had no difficulty maintaining fixation throughout the course of a block of trials.

2.2. Results

The difference thresholds and PSE data for each of JW's sessions are reported in Table 1. His threshold data are also presented in Fig. 3a as coefficient of variation (CoV) scores, calculated by dividing the difference threshold by the standard duration. The threshold and PSE data were statistically analyzed using a repeated-measures ANOVA in which the

Table 1
Difference thresholds and PSE values for JW from each session in Experiment 1 (interval discrimination)

Session	Left hand		Right hand	
	Left VF	Right VF	Left VF	Right VF
Difference thresholds				
1	64	64	86	93
2	100	64	150	143
3	79	86	93	100
4	114	50	200	179
5	86	114	129	207
6 ^a	71	271	171	257
Mean	85.7	108.2	138.2	163.2
S.D.	18.6	82.9	44.5	63.7
PSE values				
1	478	493	600	550
2	543	593	850	714
3	407	571	521	600
4	443	578	728	821
5	628	643	685	750
6 ^a	600	721	828	743
Mean	516.5	599.8	702.0	696.3
S.D.	88.3	76.6	128.0	101.6

Values are reported in ms, and were derived by multiplying the number of raster cycles by the number of ms per raster cycle (14.28). The reference duration was 571 ms.

^a Denotes session performed with eye-tracking.

visual field of the comparison interval and the hand of response were treated as within-subjects factors, with the six experimental sessions as the random factor. As can be seen in Fig. 3a, the difference threshold was lower when JW responded with his left hand, ($F(1, 5) = 15.20$, $P < 0.05$). However, the main effect of visual field, ($F(1, 5) < 1.0$),

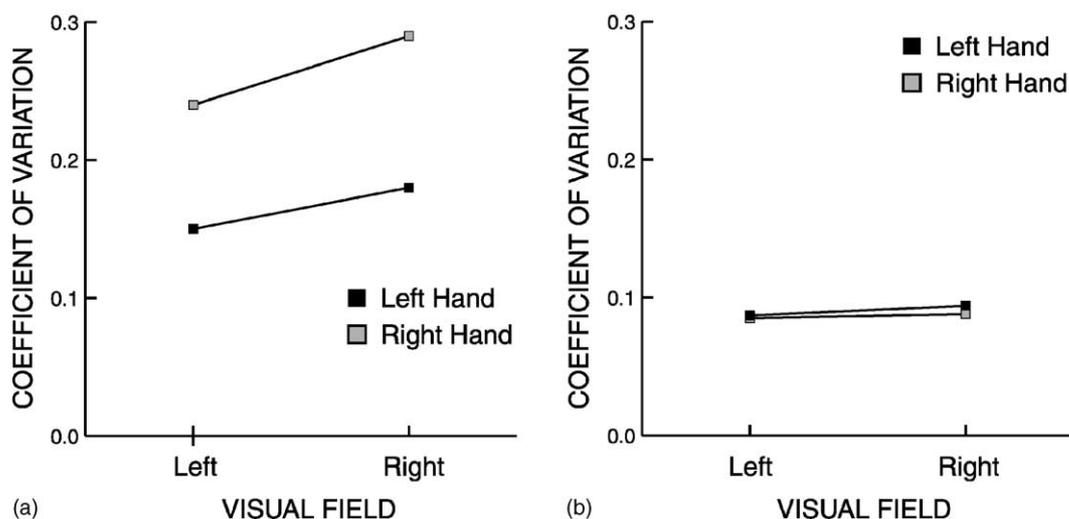


Fig. 3. Plot of the CoV scores from the interval discrimination task in Experiment 1. The standard duration was 571 ms. (a) JW's left hand was more accurate in performing the task than his right hand, suggesting that his right cerebral hemisphere has an advantage over his left in discriminating interval durations. There was no interaction between hand of response and visual field of target. (b) Data for the control participants, showing no hand by visual field interaction. Note: A smaller CoV score indicates greater discrimination accuracy.

Table 2
Difference thresholds and PSE values for each control participant in Experiment 1 (interval discrimination)

Subject	Left hand		Right hand	
	LVF	RVF	LVF	RVF
Difference thresholds				
1	59	59	30	44
2	37	59	30	44
3	81	59	67	37
4	30	44	74	81
Mean	51.8	55.5	50.0	51.8
S.D.	23.4	7.4	23.7	20.0
PSE values				
1	577	577	607	577
2	599	592	681	636
3	688	666	673	703
4	725	681	696	659
Mean	647.3	629.0	664.3	643.8
S.D.	70.6	52.1	39.3	52.5

Values are reported in ms, and were derived by multiplying the number of raster cycles by the number of ms per raster cycle (14.28). The reference duration was 571 ms.

and most importantly, the hand \times visual field interaction, ($F(1, 5) < 1.0$), did not approach significance.

For JWs PSE data, there was a significant main effect of hand ($F(1, 5) = 18.83$, $P < 0.01$), indicating that there was a bias to respond “LONG” when using the left hand relative to the right hand. The interaction between the hand of response and visual field of the target approached significance ($F(1, 5) = 5.25$, $P < 0.08$), suggesting that this bias was greater when the comparison stimulus was presented in the left visual field, the side congruent with the responding hand. There was no main effect of visual field ($F(1, 5) = 1.99$).

The difference thresholds and PSE values for the control participants are reported in Table 2, and their CoV scores are plotted in Fig. 3b. Repeated-measures ANOVAs performed on the difference thresholds and PSE values showed no main effects or interactions approaching significance.

2.3. Discussion

In terms of JWs temporal acuity, there was no indication of an interaction between response hand and visual field. Thus, the results are inconsistent with the hypothesis that temporal representations are lateralized. Instead, JWs difference thresholds showed only a significant effect of response hand, with the left hand responding more accurately than the right. These findings suggest a number of constraints in terms of the architecture for processes involved in making duration judgments. First, the lack of a visual field effect and the absence of a visual field by response hand interaction in both JW and the control participants suggest that the temporal representations are accessible bilaterally in cortex, on the assumption that the decision processes are

cortical. This result points to the involvement of subcortical structures in task-related processes, given that the callosotomy operation has eliminated direct interhemispheric communication.

Second, in contrast to the control participants who showed no asymmetry in accuracy discrimination, JWs performance was significantly more accurate when responses were made with his left hand. This pattern suggests two possible explanations. One, the left hemisphere may simply not have adequate access to the requisite temporal representations. In other words, regardless of how these representations are lateralized subcortically, there may be preferential projection to the right cerebral hemisphere. As a consequence, the left hand would outperform the right hand independent of the visual field of the comparison interval.

Alternatively, there may be a right hemisphere advantage in the retention and comparison components of the task. The inferior performance of the left hemisphere would thus not be attributed to a lack of temporal information per se. Rather, it would reflect an impairment in the ability to retain and compare the duration representations. In short, the working memory capacities of the right hemisphere may be more optimally tuned to duration judgments than the working memory capacities of the left hemisphere. This hypothesis would explain the main effect of response hand in JWs discrimination accuracy. It would also account for the differential bias observed for the two response hand conditions, based on the assumption that the representation of the standard duration is different for the two hemispheres.

The notion that the right hemisphere is specialized for the decision processes involved in making the discriminations is consistent with evidence from both neuropsychological and neuroimaging studies. In an interval discrimination task performed by patients that had unilateral cortical lesions, only the patients with right hemisphere damage were impaired (Harrington, Haaland, & Knight, 1998). Similarly, when event-related fMRI was used in normals to dissociate the brain areas associated with encoding versus comparing interval durations lasting just over 1 s, the data suggested that the right hemisphere was uniquely involved in the latter task component (Rao et al., 2001). This hypothesis is also appealing on the grounds of parsimony since it does not require positing asymmetric transfer between subcortical and cortical structures. As a consequence, we hypothesize that the representation of a lateralized comparison interval is accessible bilaterally in cortex, with a right cerebral hemisphere advantage in interval comparison- and decision-related processes.

However, despite the monitoring of JWs eye movements during one of the experimental sessions in Experiment 1 and the similarity of results between this session and the others, we can not rule out the possibility that JW was making undetected systematic eye movements in the sessions where eye movements were not tracked. Indeed, the target durations used in Experiment 1 were sufficiently long to allow for saccades to the target while it was still present. The

lack of a hand by visual field interaction could result from undetected saccades that allow bilateral projection from a foveated comparison stimulus. To address this concern, a second experiment was performed in which the durations of the stimuli used were greatly reduced.

3. Experiment 2

The standard interval was reduced to 150 ms in Experiment 2. This allowed us to repeat our initial experiment while asking two critical questions. First, could the results of Experiment 1 be replicated? Replication is especially important here since the main evidence supporting our hypothesis rests on a null result—the lack of an interaction between the visual field of the comparison stimulus and the response hand. Second, by using shorter standard and comparison interval durations, we could avoid problems that might arise should JW be making eye movements following the onset of the lateralized comparison stimulus. Because it takes about 200 ms to saccade to a stimulus, the comparison stimulus would be terminated before any eye movements would be completed.

3.1. Method

All participants, methods, and procedures were identical to Experiment 1, with the following exceptions. The stimuli were three red LEDs mounted on a vertically-standing board. The LEDs were aligned in a horizontal row, with the center LED serving as the fixation point. The LEDs on either side of fixation were at the same approximate distance from fixation as the locations of the standard and target bars in Experiment 1. The use of LEDs allowed for millisecond-level control of stimulus durations, a level of temporal precision not available with standard VGA monitors, as well as minimization of stimulus persistence.

The general procedure was as in Experiment 1. 1000 ms after the onset of a central fixation LED, the two lateral LEDs were illuminated for 150 ms, defining the standard interval duration. Following an 1100 ms delay, one of the two lateral LEDs was turned on, either a shorter or longer duration than the standard interval. Based on pilot work, we adopted a step size of 4 ms for the PEST procedure. The duration of the comparison stimulus was set to a 100 ms difference from the standard for the first set of practice trials and 60 ms for the second set of practice trials. As in Experiment 1, the standard and comparison durations were equal on the last practice trial for each visual field.

3.2. Results

The difference thresholds and PSE data from each of JW's sessions in Experiment 2 are reported in Table 3, and his corresponding CoV scores are plotted in Fig. 4a. An omnibus repeated-measures ANOVA was performed on the difference

Table 3
Difference thresholds and PSE values for JW from each session in Experiment 2 (interval discrimination)

Session	Left hand		Right hand	
	Left VF	Right VF	Left VF	Right VF
Difference thresholds				
1	40	50	76	68
2	44	48	42	40
3	22	30	30	44
4	22	34	50	46
5	30	42	34	34
6	32	36	44	60
Mean	31.7	40.0	46.0	48.7
S.D.	9.1	8.0	16.3	12.8
PSE values				
1	202	148	194	154
2	150	170	216	146
3	140	120	184	166
4	136	188	220	224
5	172	132	236	224
6	150	130	222	206
Mean	158.3	148.0	212.0	186.7
S.D.	24.8	26.3	19.3	35.5

Values are reported in ms. The standard duration was 150 ms.

thresholds with the factors response hand (left versus right) and visual hemifield of target bar (left versus right). There was a significant main effect of visual field ($F(1, 5) = 9.68$; $P < 0.05$) and a marginally-significant main effect of hand of response ($F(1, 5) = 4.92$; $P < 0.08$), with performance superior when the responses were made with the left hand. Importantly, there was again no indication of a hand \times visual field interaction ($F(1, 5) = 1.25$).

For JW's PSE data there was again a significant main effect of hand ($F(1, 5) = 13.21$, $P < 0.05$), indicating a tendency to respond "longer" when using the left compared to the right hand. However, there was no main effect of visual field ($F(1, 5) = 3.11$) and no significant interaction between visual field and hand of response ($F(1, 5) = 0.67$).

The difference thresholds and PSE values for the control participants are reported in Table 4, and their CoV scores are plotted in Fig. 4b. Repeated-measures ANOVAs performed on the difference thresholds and PSE values showed only a main effects of visual field approach significance ($F(1, 3) = 7.36$, $P < 0.08$) in the PSE data.

3.3. Discussion

The results from Experiment 2 essentially replicate the results of Experiment 1. Supporting the hypothesis that temporal coding involves subcortical structures, JW and the controls both again failed to show an interaction between the visual field of the comparison stimulus and the hand making the response. Given the short (<200 ms) standard and target durations used in Experiment 2, this convergence of results

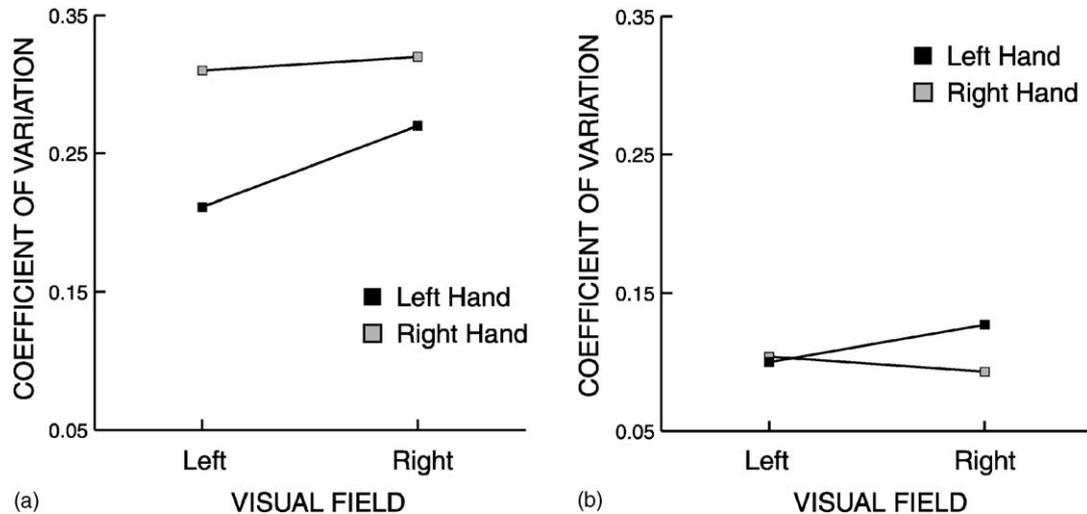


Fig. 4. Plot of the CoV scores from the interval discrimination task in Experiment 2. The standard duration was 150 ms. (a) Again there was no interaction between JW's hand of response and the visual field of target. Rather, JW's left hand again showed greater accuracy on the task, relative to his right hand. (b) Data for the control participants, showing no hand by visual field interaction.

between experiments is inconsistent with the proposal that JW's results from Experiment 1 could be explained by undetected saccades to the target. Moreover, that similar data patterns were observed in the two experiments suggests that the results of Experiment 1 were not idiosyncratic to the specific durations used in that experiment.

Taken together, two key points emerge from our initial experiments. First, temporal judgments of lateralized stimuli appear to be accessible bilaterally in cortex. We suggest that the first observation is consistent with subcortical involvement in providing the requisite temporal representations of the stimuli, representations which are then accessi-

ble to both cerebral hemispheres. Second, JW's performance was more accurate when the comparison stimulus was presented to the left visual field and, similar to Experiment 1, when the left hand was used to make the responses. We hypothesize that the right hemisphere superiority in JW reflects operations associated with the comparison and decision processes, perhaps reflecting attentional and/or working memory operations related to maintaining the representation of the standard interval duration (Rao, Mayer, & Harrington, 2001). Supporting this hypothesis, the control participants never showed evidence of a similar laterality, likely due to their rapid and efficient ability to communicate task-relevant information between the cerebral hemispheres via intact callosal fibers.

While the consistent difference between hands in JW's PSE scores may be tied to biases associated with responding (e.g. idiosyncratic preferences for each hand in terms of the response per se), these biases may also reflect an asymmetry in the remembered duration of the standard. For example, the memory of the standard in the right hemisphere may decay faster relative to the left hemisphere, leading to a bias to perceive the comparison stimulus as longer. Regardless, performance is not limited by the transfer of temporal representations from subcortical to cortical structures, but is instead constrained by hemispheric differences in the ability to maintain and compare these representations.

4. Experiment 3

To this point, we have sketched a series of hypothetical operations assumed to be invoked in the course of judging interval durations. Some of these operations are specific to temporal processing. For example, we assume an internal timing mechanism is essential for deriving representations

Table 4

Difference thresholds and PSE values for each control participant in Experiment 2 (interval discrimination)

Subject	Left hand		Right hand	
	Left VF	Right VF	Left VF	Right VF
Difference thresholds				
1	10	26	12	20
2	18	24	22	14
3	20	14	4	14
4	14	12	24	8
Mean	15.5	19.0	15.5	14.0
S.D.	4.43	7.02	9.29	4.90
PSE values				
1	136	152	162	146
2	156	146	144	164
3	182	180	166	184
4	196	202	190	194
Mean	167.5	170.0	165.5	172.0
S.D.	26.8	26.0	18.9	21.4

Values are reported in ms. The standard duration was 150 ms.

of stimulus durations. However, some operations used for interval discriminations may generalize to other tasks as well. Within this context, we cannot say with certainty that the right hemisphere task advantage observed for JW in the two preceding experiments is specific to temporal processing tasks. That is, his right hemisphere advantage in task performance may be evident whenever a comparison is required between two successive events.

In Experiment 3, we tested JW on two versions of a non-temporal perceptual judgment task. Similar to Experiment 1, the standard stimulus consisted of two vertical bars, one in the left visual field and one in the right visual field. Following a brief delay, a single vertical bar was presented in one of the two visual fields. Rather than manipulate the duration of the comparison bar, we now varied its height (or size). JW was required to judge if the size of the lateralized comparison bar was shorter or longer than the size of the bilaterally-presented standard bars.

Adopting this paradigm, Experiment 3 allowed us to test the domain specificity of the results obtained in Experiments 1 and 2. First, we could assess whether an interaction between the visual field of the comparison bar and the hand of response would be found in JW on a task requiring the assessment of a non-temporal stimulus property. Models of visual perception assume that representations of object form are cortically derived (Farah, 1990; Ungerleider & Mishkin, 1982). Based on this assumption, we predicted that JW's performance in Experiment 3 would be better when his hand of response was ipsilateral to the visual field of the comparison bar, relative to when they were contralateral to each other. The lack of such an interaction would suggest that the bilateral availability of lateralized visual information is not specific to temporal representations.

Second, the results of Experiment 3 would indicate if the right hemisphere advantage observed in the first two studies is specific to temporal processing tasks. For example, it has been reported that patients with RH lesions were specifically impaired on a duration discrimination task (Harrington et al., 1998). In comparison, patients with lesions in left frontal cortex tended to perform worse relative to RH patients in a frequency discrimination task, suggesting that RH patients were selectively impaired in the duration task. By using a non-temporal discrimination task in Experiment 3, we could similarly assess whether the observed hemispheric asymmetries in Experiments 1 and 2 were specific to temporal processing tasks as well.

4.1. Method

All participants, methods, and procedures were identical to Experiment 1, with the following exceptions. The height of the standard bars was increased to 10.4° , and the height of the comparison bar was varied across trials. JW was required to judge whether the height (size) of the comparison bar was shorter or longer than the size of the pair of standard bars, with the PEST procedure again set to determine thresh-

olds at which JW was correct on 75% of the trials. The step size used in this procedure was two pixels, or approximately 0.1° of visual angle. To maintain congruency with Experiments 1 and 2, two different exposure durations were used, varied between sessions. In the short duration sessions, the exposure duration of the bars was fixed at 143 ms (approximating the duration of the standard interval in Experiment 2). In the long duration sessions, the exposure duration of the bars was 571 ms (the duration of the standard interval in Experiment 1). Eye movements were monitored during one of JW's sessions in the long duration condition. This session confirmed that JW could perform the task without making saccades to the target.

4.2. Results

The difference thresholds and PSE values from each of JW's sessions in Experiment 3 are reported in Table 5 as a function of the duration condition, and his CoV scores are plotted in Fig. 5a. An omnibus repeated-measures ANOVA was performed on JW's difference thresholds that had stimulus duration (short versus long), hand of response (left versus right), and visual hemifield of the comparison stimulus (left versus right) as factors. Importantly, the ANOVA results indicated that there was a significant interaction between the visual field of the comparison stimulus and the hand used to make the responses ($F(1, 5) = 16.37$; $P < 0.01$).

Table 5
Difference thresholds and PSE values for JW from each session in Experiment 3 (size discrimination)

Session	Short duration				Long duration			
	Left hand		Right hand		Left hand		Right hand	
	LVF	RVF	LVF	RVF	LVF	RVF	LVF	RVF
Difference thresholds								
1	12	20	35	13	6	7	11	5
2	5	9	26	27	8	12	18	11
3	7	9	23	15	7	4	6	7
4	28	5	39	10	7	30	21	15
5 ^a	19	19	41	19	7	8	5	6
6	6	7	8	4	7	10	8	4
Mean	12.8	11.5	28.7	14.7	7.0	11.8	11.5	8.0
S.D.	9.1	6.4	12.4	7.9	0.6	9.3	6.6	4.2
PSE values								
1	182	188	215	205	184	211	217	201
2	197	195	212	211	198	210	216	201
3	183	201	207	205	193	208	214	205
4	188	175	221	208	193	218	217	199
5 ^a	173	207	207	205	207	210	215	204
6	186	207	216	208	195	200	208	204
Mean	184.8	195.5	213.0	207.0	195.0	209.5	214.5	202.3
S.D.	7.9	12.4	5.5	2.4	7.5	5.8	3.4	2.3

Values are reported in pixels and the height of the standard was 200 pixels.

^a Denotes session performed with eye-tracking in the long duration condition.

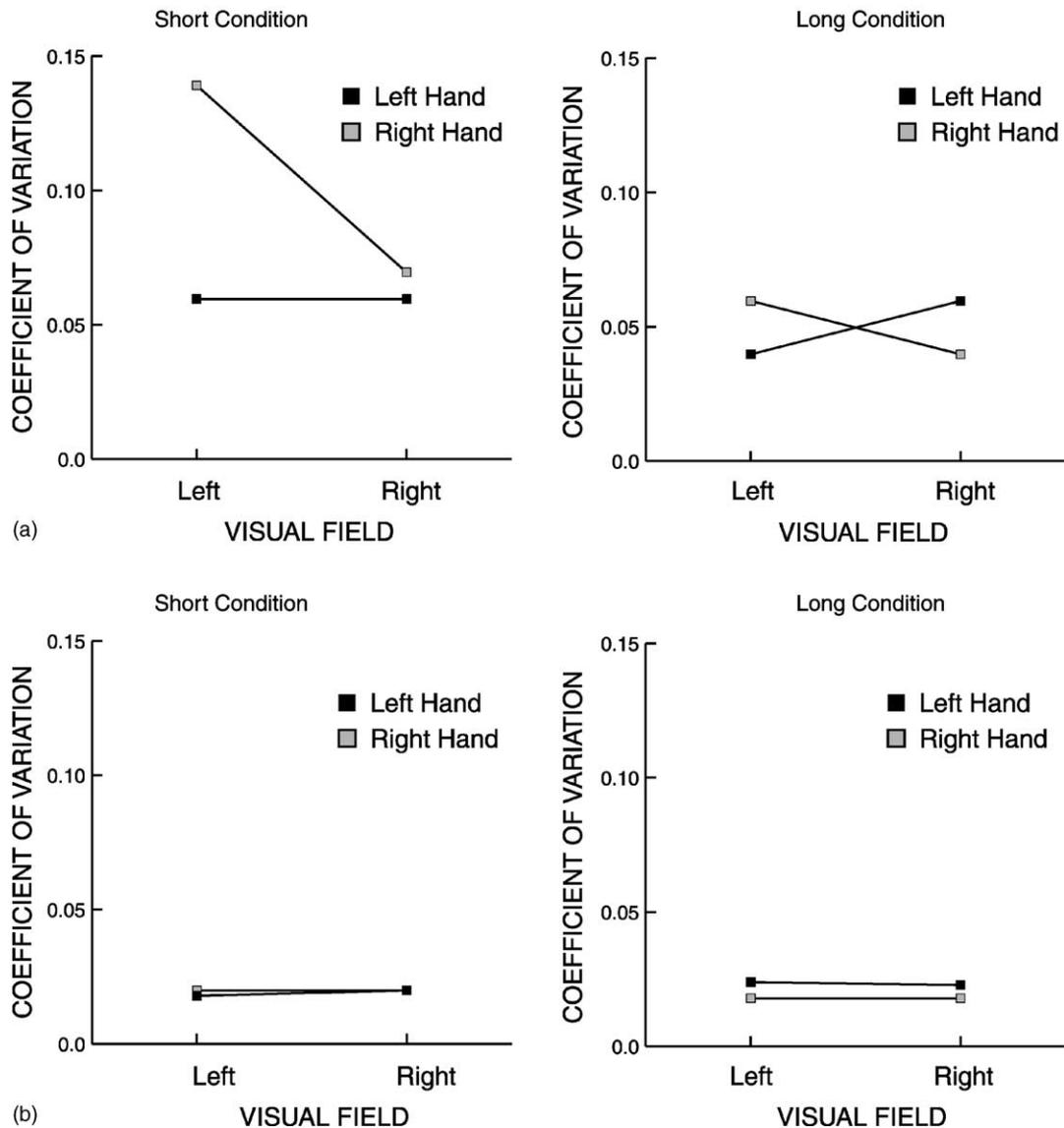


Fig. 5. Plot of the CoV scores from the size discrimination task in Experiment 3. In the short condition the standard and target bars were presented for 141 ms, and in the long condition the bars were presented for 571 ms. (a) In contrast to the data from Experiments 1 and 2, the data from Experiment 3 showed an interaction between JW's hand of response and the visual field of the target in both the short (left) and long (right) presentation conditions. (b) Data from the control participants, showing no hand by visual field interaction in either presentation condition. These data support the assumption that the interactions observed in JW's data were due to a lack of callosal communication between his cerebral hemispheres.

Although Fig. 5a suggests a different pattern was manifest for the short and long duration conditions, the three-way interaction did not approach significance ($F(1, 5) = 0.33$). Significant effects were also obtained for the response hand ($F(1, 5) = 7.71$; $P < 0.05$) and the hand by duration interaction ($F(1, 5) = 23.27$; $P < 0.005$). JW's performance with the right hand improved in the long duration condition, reaching the level of that observed with his left hand. The response hand by visual field interaction approached significance ($F(1, 5) = 6.58$; $P < 0.06$), reflecting JW's poorer performance when responding to a comparison bar in the left visual field with the right hand.

For JW's PSE values, an omnibus repeated-measures ANOVA revealed significant main effects of duration

($F(1, 5) = 7.27$; $P < 0.05$), response hand ($F(1, 5) = 61.36$; $P < 0.05$), and a significant interaction of these two factors, ($F(1, 5) = 13.61$; $P < 0.05$). As in Experiments 1 and 2, JW was biased to respond "LONG" when responding with the left hand and this bias became more pronounced when the stimuli were presented in the short duration condition. There was also a significant response hand by visual field interaction ($F(1, 5) = 90.96$; $P < 0.0005$).

The difference thresholds and PSE values for the control participants are reported in Table 6, and their CoV scores are plotted in Fig. 5b. Repeated-measures ANOVAs performed on the difference thresholds and PSE values showed no main effects or interactions that approached significance.

Table 6
Difference thresholds and PSE values for each control participant from Experiment 3 (size discrimination)

Subject	Left hand		Right hand		Left hand		Right hand	
	LVF	RVF	LVF	RVF	LVF	RVF	LVF	RVF
Difference thresholds								
1	2	4	2	1	2	3	2	3
2	5	4	4	7	8	8	5	2
3	2	4	5	2	3	3	3	4
4	5	4	5	6	6	8	4	5
Mean	3.5	4.0	4.0	4.0	4.8	5.5	3.5	3.5
S.D.	1.7	0.0	1.4	2.9	2.8	2.9	1.3	1.3
PSE values								
1	198	196	192	195	196	197	196	197
2	197	184	196	183	202	194	195	190
3	196	206	199	208	203	211	199	204
4	197	184	189	184	188	184	192	191
Mean	197.0	192.5	194.0	192.5	197.3	196.5	195.5	195.5
S.D.	0.8	10.6	4.4	11.7	6.9	11.2	2.9	6.5

Values are reported in pixels and the height of the standard was 200 pixels.

4.3. Discussion

For both duration conditions, JW's performance was better when the comparison bar and the hand of response side were congruent (Fig. 5a). In the long duration condition, the two functions cross-over; in the short duration condition, JW's performance was superior overall with the left hand, although this advantage was greatly attenuated when the comparison bar was presented in the right visual field. In this sense, his results from Experiment 3 differ from those reported in Experiments 1 and 2 in a critical way. The interaction between his hand of response and comparison stimulus location was not significant in either of the duration discrimination experiments. In contrast, Experiment 3 revealed that JW was more accurate in making size judgments when the hand used to respond was on the same side as the comparison stimulus. However, unlike JW, the control participants showed no evidence suggestive of a comparable interaction in their size discrimination accuracy (Fig. 5b). This finding supports our conclusion that the interaction observed in JW was due to the absence of callosal fibers for the transfer of lateralized object form representations between the cerebral hemispheres.

We had proposed that this pattern in JW would result if the stimulus and response information were being generated in the same hemisphere. Thus, the data are consistent with the idea that size (or object form) representations are lateralized in cortex, and that this information must be transferred over indirect (and presumably noisy) sub-cortical pathways for interhemispheric communication in the split-brain. Although the interaction might reflect other processing architectures (e.g. noisy ipsilateral control of the responses compared to more standard contralateral control

of the responses), the findings do indicate that the null interaction results observed for JW in Experiments 1 and 2 are not generic to all psychophysical judgments between two sequential stimuli. Whereas the correspondence of comparison stimulus location and response hand is not important when JW makes judgments based on stimulus duration, it is integral when making judgments based on stimulus size.¹

On the other hand, two aspects of the results of Experiment 3 are similar to those of Experiments 1 and 2. First, JW again exhibited superior performance with the left hand, although this advantage in making length judgments was limited to the short duration condition. Assuming that this effect reflects a right hemisphere advantage, it would appear that this advantage is not limited to temporal processing tasks. Rather, it may reflect some basic asymmetry between the two hemispheres in their ability to compare successive events, perhaps related to the working memory requirements associated with the retrieval of information about the standard stimulus and/or decision processes. Again, a similar effect was absent in the control participants, presumably due to their ability to communicate information transcallosally.

Second, we also observed a similar pattern in the biases across the duration and size discrimination tasks. Comparison stimuli were more likely to be judged "LONG" when responses were made with the left hand. Given that we did not manipulate the mapping of the response labels and response keys (to minimize memory demands on JW), it is possible that these biases reflect idiosyncrasies in finger preferences for the two hands. Alternatively, the biases may instead result from abstract representations of the concepts "SHORT" and "LONG", even though these terms were used to capture different properties of the stimuli (duration or size). For example, if the representation of the standard stimulus was to decay faster in the right hemisphere, subsequent stimuli might be judged as longer in time or size.²

5. General discussion

Using visual stimuli to signal time intervals, split-brain patient JW was asked to compare the duration of a standard stimulus that was presented bilaterally with a comparison stimulus that was restricted to either the left or right visual

¹ Even though a hand by visual field interaction was observed in Experiment 3, the data indicate that the hemisphere not directly viewing the comparison stimulus was nevertheless able to perform the task well above chance levels. This finding is consistent with the proposal that the split hemispheres may be capable of rapidly communicating binary information (e.g. "shorter" versus "longer") despite the absence of callosal connections (Corballis, 1994).

² This idea would assume that the representation of a stimulus fades over time in the manner of a Cheshire Cat, with its remembered time or length slowly fading to nothing. We are not aware of evidence in favor of such a view of memory decay; our point here was to offer one example as to how asymmetric processes could produce similar bias patterns for two very different uses of length-based adjectives.

field. The hand used to make the response was varied between trial blocks. Assuming the contralateral cerebral hemisphere controls the response hand, a hand by visual field interaction was expected if the representation of stimulus duration was restricted to the hemisphere receiving the lateralized stimulus. However, we failed to observe this interaction for two different ranges of stimulus durations, both in the hundred (Experiment 2) to hundreds (Experiment 1) of milliseconds range. Instead, JW always performed the temporal discrimination task more accurately when his left hand was responding, an asymmetry in performance that was absent in the control participants. These results suggested a bilateral representation of stimulus duration in cortex, with a right hemisphere advantage in the working memory component of the task (see also (Kagerer, Wittmann, Szelag, & Steinbüchel, 2002)). In contrast, when JW made a discrimination based on the length of the stimuli rather than their duration, an interaction between response hand and visual field was obtained (Experiment 3). Specifically, the difference thresholds were lower when the response hand was ipsilateral to the visual field of the comparison stimulus.

The lack of hand by visual field interaction on the duration tasks is consistent with the conclusion that subcortical structures play a critical role in the representation of temporal information. As outlined in the Introduction, both the cerebellum and basal ganglia appear to be integral to the representation of temporal information (reviewed in (Ivry, 1996; Malapani et al., 1998; Mangels & Ivry, 2001)). Taken in this light, it is important to caution that our results do not necessarily contribute to the debate regarding the relative contribution of these two structures to the formation of temporal representations. Our results do, however, suggest that subcortically-derived temporal representations are accessible bilaterally in cortex even when the input is lateralized. The cerebral hemispheres cannot communicate directly in the split-brain, yet independent of his hand of response JW's performance in the duration task was unaffected by the visual field of the target stimulus. This indicates that subcortical temporal representations can be directly projected to both cerebral hemispheres, without the need to communicate information transcallosally.

Importantly, this conclusion is supported by a neuroanatomical record which suggests that any lateralized temporal representations derived in the cerebellum and basal ganglia may be available to both halves of the cerebral hemispheres. This may arise due to the nature of the sensory input to these structures, the subsequent cortical projections from these structures, or both. For example, each hemisphere of the cerebellum receives visual input from both the ipsilateral and contralateral visual field. As shown in the cat, the dorsolateral pontine nucleus receives input from the superior colliculus and projects to the ipsilateral cerebellar hemisphere, while the medial pontine nucleus receives input from visual cortex and projects to the contralateral cerebellar hemisphere (Mower, Gibson, Robinson, Stein, & Glickstein, 1980). As a consequence,

each cerebellar hemisphere would thus have the requisite visual input to derive a representation of stimulus duration independent of the visual field of presentation.

On the other hand, visual input into the basal ganglia may remain lateralized, as the striatum appears to receive only lateralized projections from visual cortical areas, such as TE and MT (Cheng, Saleem, & Tanaka, 1997; Weller, Steele, & Kaas, 2002). However, it has been shown in non-human primates that striato-thalamic projections are bilateral in nature (Parent, Lévesque, & Parent, 2001; Parent, Lévesque, & Parent, 1999), thereby, providing the means by which a lateralized temporal representation in the striatum could then be represented bilaterally at the level of the thalamus. Once at the thalamic level, temporal representations derived in either the cerebellum or basal ganglia can then be bilaterally projected to a number of higher cortical regions—including working memory areas in dorsolateral prefrontal cortex—via crossed and uncrossed cerebello-thalamocortical and pallido-thalamocortical pathways (Alexander, DeLong, & Strick, 1986; McFarland & Haber, 2002; Middleton & Strick, 1994; Middleton & Strick, 1998; Middleton & Strick, 2000; Schmahmann & Pandya, 1997).

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