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(Article begins on next page)

Visual Spatial Attention and Visual Short-term Memory: Electro-magnetic Explorations of Mind.

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Visual short-term memory has a very limited storage capacity of about three objects. Some stages of categorization and decision making appear also to have very sharp capacity limitations, sometimes as low as one representation. Early visual processing, on the other hand, is massively parallel and can deliver many more stimuli for further processing than can be stored or acted upon. In this chapter we review recent work from our laboratories that explores how early and late attentional mechanisms interact to select and store information of interest to the observer. The studies are based on the analysis of electrophysiological and magnetoencephalographic recordings using paradigms that allowed us to track the moment to moment deployment of visual spatial attention and the participation of visual short-term memory in ongoing cognitive processing. These studies showed that visual spatial attention modulates early cortical responses to attended stimuli, whether attention was deployed voluntarily or involuntarily, that the deployment of spatial attention is impaired by concurrent processing in the attentional blink and psychological refractory period paradigms, and that transfer to visual short term memory is impaired and/or delayed by concurrent central processing. Finally, converging evidence from functional magnetic resonance imaging, event-related potentials, event-related magnetic fields, and time-frequency analysis of magnetoencephalography data, showed that activity of neurons in parietal cortex play an important role in the representations of objects in visual short-term memory.

For thousands of years, thoughtful men and women have wondered how human beings perceive the world through vision, hearing, and other senses, and how they feel, remember, and think. Recent advances in physics, engineering, and psychology, are enabling cognitive neuroscientists to provide answers with heretofore unparalleled accuracy and detail to these fundamental questions concerning the human psyche. In this chapter we summarize recent work that combines basic methods of cognitive psychology with recent advances in electrophysiology, magnetoencephalography, and functional magnetic resonance imaging, that illustrates how the convergence of these methods is enabling us to understand basic mechanisms of human visuospatial attention and visual short-term memory at the functional and neural levels.

Despite the wondrous complexity of the human brain, we are often severely limited in how we perceive and process information about the world. Although we would often like to think about every possible thought, at the same time, there is ample empirical evidence to confirm the common-sense conclusion based on everyday experience that we can only entertain a small number of ideas at any given time. The number of ideas that we can entertain at the same time, in some cases, appears to be as few as one. On the other hand, it is clear that the world often affords us the opportunity to process a great many different stimuli, each of which capable of triggering a cascade of perceptions, object recognitions, associated memories, and reflections. Somewhere between the image on the retina and conscious awareness, there are massive restrictions in the transmission of information and restrictions in terms of representational and storage capacity that limit what we can perceive and remember from a visual scene.

Psychophysical studies have shown that the storage capacity of visual short-term memory is about three objects, on average (Vogel, Woodman, & Luck, 2001; see also Cowan, 2001). Given the severe processing rate and storage capacity limitations in later stages of processing, attentional selection of a subset of the possible inputs for further processing is often desirable (Sperling, 1960). In this chapter we summarize recent work

that enables us to track encoding and maintenance of information in visual short-term memory.

Visual spatial attention consists of a set of mechanisms that selects one or more locations in the visual display for further processing. The selected information can then be subjected to more detailed processing, possibly leading to an overt response, and/or to storage in one or more types of memory. Single-cell electrophysiology has shown that the firing rate of cells in early visual cortex (i.e., as early as V1) increases when the cell participates in the processing of an attended stimulus (Roelfsema & Spekreijse, 2001). Interestingly, recent work using human electrophysiology has revealed a component of the event-related potential, called the N2pc, that appears to be a correlate of the deployment of visuospatial attention to lateralized visual stimuli (Luck & Hillyard, 1994). Another event-related potential component, which we call the sustained posterior contralateral negativity (SPCN), tracks the involvement of visual short-term memory in stimulus processing (Jolicœur, Sessa, Dell'Acqua, & Robitaille, 2006a). The chapter is divided into two major parts. In the first part of the chapter we describe the N2pc and recent work showing how we can use this component to determine when and how subjects can or cannot deploy visuospatial attention to a visual target. In the second part we review recent work focusing on the SPCN as an index of visual short-term memory.

THE ATTENTIONAL BLINK AND VISUAL SPATIAL ATTENTION.

Impaired deployment of spatial attention during the attentional blink.

Recent work in our laboratories focused on the ability to deploy visual spatial attention to a second visual target (in the periphery) while processing of another, previously-presented, target was still ongoing, during the period of the attentional blink. Initially, our motivation was to demonstrate the independence of the attentional blink and visual spa-

tial attention. The independence assumption was based on previous work that had shown that the attentional blink appeared to be confined to relatively late stages of processing, such as the short-term consolidation of information in memory (Jolicœur, 1998; Jolicœur & Dell'Acqua, 1998; Sessa, Luria, Verleger, & Dell'Acqua, 2007; Vogel, Luck, & Shapiro, 1998). We quickly discovered that our initial assumption of independence between the attentional blink and the ability to deploy visuospatial attention was incorrect, however, as we summarize below.

In the attentional blink paradigm there are usually two targets, T_1 and T_2 , presented briefly and each followed by a mask, often in the context of other distractor stimuli presented using rapid serial visual presentation. Jolicœur et al. (2006a) modified the attentional blink procedure, as illustrated in Figure 1, enabling them to use human electro-physiology to track the deployment of spatial attention and encoding in visual short-term memory associated with the processing of the second target. In the initial portion of each trial we presented a sequence of distractor letters at fixation at a rate of 10 items per second. One of the letters in the sequence was replaced by a digit, and this was the first target, or T_1 . The degree of central processing involvement was manipulated by instructing subjects either to encode and remember this digit (report- T_1), or to ignore it (ignore- T_1). The second target, T_2 , was presented following T_1 after either one additional item in the central stream (lag 2, at a stimulus onset asynchrony, or SOA, of 200 ms, illustrated in Figure 1) or after seven additional items (lag 8, SOA of 800 ms). T_2 was also a digit and it was presented either to the left or right of fixation, and was either red (for half of the subjects) or green (for the others). Another digit was presented concurrently with T_2 on the other side of fixation, and in the other colour (e.g., in green if the target was red). The two digits in the T_2 time frame were followed by a bilateral mask (the letter W) to ensure that we would observe an attentional blink (Giesbrecht & Di Lollo, 1998; Jolicœur, 1999b). The task, for T_2 , was to encode and later report the identity of T_2 , without moving the eyes. Recordings of the horizontal oculogram allowed us to verify that no subject moved

their eyes more than $.2^\circ$ in the direction of the target, on average.

Insert Figure 1 About Here

The logic of the design was as follows. In the report- T_1 condition, encoding T_1 should occupy central mechanisms and this should produce the conditions required to observe an attentional blink (e.g., Jolicœur, 1999a; Vogel et al., 1998). When T_2 is presented at lag 2, only a short time after T_1 , some aspect of the processing of T_2 suffers because a central mechanism or capacity is occupied by the ongoing processing of T_1 (Jolicœur, 1999a). When T_2 is presented at lag 8, and thus relatively long after T_1 , the encoding of T_1 should be completed and any interference on T_2 would likely be attributable to the load of maintaining a memory representation of T_1 until the end of the trial (Jolicœur & Dell'Acqua, 1998).

Trial blocks in which T_1 could be ignored provided a control condition with identical physical stimulation as in the report- T_1 condition, but without the processing costs associated with the encoding and retention of a representation of T_1 (Jolicœur, 1999a; Raymond, Shapiro, & Arnell, 1992).

But, how would we know whether subjects succeeded or failed to deploy visuospatial attention to T_2 ? The behavioural results alone would be ambiguous. Failing to report the correct identity of T_2 could occur because of a failure to deploy attention to T_2 or to a failure at later stages of processing (e.g., memory encoding) despite successful deployment of spatial attention.

This is where we capitalized on the potential of human electrophysiology to track processing at intermediate stages of processing between stimulus and response. The selection of a visual target for further processing is often associated with an electrophysiological response, called the N2pc, that has been studied extensively by several researchers, and most particularly by Luck and his colleagues (e.g., Dell'Acqua, Pesciarelli, Jolicœur, Eimer, & Peressotti, 2007; Eimer, 1996; Girelli & Luck, 1997; Jolicœur, Sessa, Dell'Acqua, & Ro-

bitaille, 2006a; Luck, Girelli, McDermott, & Ford, 1997; Luck & Hillyard, 1994; Woodman & Luck, 2003). The N2pc event-related potential (ERP) is a lateralized response characterized by a greater negativity over the hemisphere contralateral to the visual field of a target relative to the response over the hemisphere ipsilateral to the target. The N2pc difference waveform, computed by subtracting the ipsilateral from the contralateral responses of corresponding electrode pairs positioned symmetrically about the midline (e.g., T5, T6; O1, O2; Jasper, 1958) for lateralized visual targets, is usually found from about 180 ms to 280 ms post target onset and is maximal at posterior electrode sites (often between O1 and T5, and O2 and T6, in the 10-20 system, Jasper, 1958, or PO7/PO8 as this position is named in the 10-10 system, American Electroencephalographic Society, 1994; see, e.g., Brisson & Jolicœur, 2007a, 2007b; Luck & Hillyard, 1994; Robitaille & Jolicœur, 2006a). Note that we used a minimum of 200 trials per condition (for each subject) in experiments in which the N2pc component was measured, to ensure an adequate signal-to-noise ratio in the event-related electrophysiological results. This is many times more trials per condition than are typically used in behavioural studies, and this often required modifications of the typical experimental designs (e.g., including fewer SOA conditions).

In short, when attention is deployed on a target in the left visual field, we should observe a greater negativity at right-sided posterior electrodes relative to the voltage recorded at corresponding left-sided electrodes. Conversely, when attention is deployed to the right, we should observe a negativity on the left relative to the voltage on the right. Woodman and Luck (2003) used the N2pc to track the deployment of visuospatial attention in the context of a visual search task. In the present work we used a simple search task in which there was one target (T_2), presented in isolation in one visual field, and one distractor, presented in the other visual field.

This combination of different paradigms allowed us to study the relationship between the mechanisms that mediate visuospatial attention and those that mediate central attentional operations. By central attention we mean operations that are post-perceptual and

encompass response selection, memory retrieval, and short-term consolidation, and that have been shown to impose large capacity demands when performed concurrently with other operations (e.g., Jolicœur & Dell'Acqua, 1998).

Other research had shown that increases in central attentional load can lead to an increase in the degree to which distracting stimuli interfere with processing of a target (de Fockert, Rees, Frith, & Lavie, 2001; Jiang & Chun, 2001). These authors argued that spatial selection is impaired when central attention is engaged on a concurrent task. This conclusion regarding spatial attention is somewhat indirect, however, because intruding information from distractors could result from a loss of control at other, later, stages of processing (e.g., response selection).

The experiment of Jolicœur et al. (2006a) provided a more direct test of the dependence or independence of the control of spatial attention on central attentional mechanisms because the N2pc can only arise as a result of a differential processing of T_2 relative to the the distractor in the T_2 visual display. The presence of this distractor is important for a number of reasons. The first was to equate the low-level sensory responses to the T_2 display across the left and right hemispheres. Had we presented T_2 by itself, large interhemispheric differences would have been observed at posterior electrode sites because of the structure of the visual system, and these interhemispheric differences would not be informative regarding the locus of visuospatial attention. Stimuli presented in the left visual field project initially only to the right hemisphere, whereas stimuli in the right visual field project initially only to the left hemisphere, in primary visual cortex (e.g., Coren, Ward, & Enns, 1994; Zeki, 1993). ERPs to a single stimulus in the left or right visual field would thus have produced large interhemispheric differences (e.g., Bayard, Gosselin, Robert, & Lassonde, 2004; Luck & Hillyard, 1994), making it more difficult to distinguish attentional effects from purely low-level sensory effects. The presence of an equivalent equiluminant form in each hemisphere produces a balanced electrophysiological response of early visual cortex across the two hemispheres (counterbalancing eliminates any small

residual differences). Differences in ERPs across the hemispheres for such displays can only arise as a function of differential processing due to attentional selection of one of the two stimuli (see Luck & Hillyard, 1994; Woodman & Luck, 2003, for further discussion).

The second reason to use a digit as a lateral distractor was to increase the probability that subjects would deploy visuospatial attention to T_2 by making the use of a late-selection strategy less useful. In order to give the correct response, subjects had to select the correct digit, namely the one in the target colour. If the display contained only one digit (say, paired with a letter), then subjects may have been able to perform the task without deploying visuospatial attention to the target location. They may have been able to use differences in semantic activation to perform the task (see Duncan, 1980, 1983). Although prior work showed that an N2pc could be observed even when a single alphanumeric character is used with a non letter distractor (e.g., Eimer, 1996), the presence of two digits in the display was meant to encourage subjects to use colour to guide visuospatial attention to one of them. Doing so would then engage differential processing at the location of T_2 , which should lead to a greater contralateral negativity at posterior electrode sites, thus producing an N2pc ERP.

Figure 2 shows the mean accuracy of report for T_2 for sixteen observers who performed a total of about 800 trials, 400 in a block in which they had to report both the identity of T_1 and T_2 , and 400 in a block in which they reported only the identity of T_2 . Within each block, trials with a lag of 2 between T_1 – T_2 (SOA of 200 ms) and trials with a lag of 8 (SOA of 800 ms) were intermixed at random. The results replicated the typical attentional blink pattern: accuracy was generally high and unaffected by lag when T_1 could be ignored, but, in contrast, accuracy decreased sharply as lag was reduced when T_1 had to be encoded and remembered for later report.

Insert Figure 2 About Here

Figure 3 shows the most important electrophysiological results. The waveforms were

computed by averaging electroencephalographic activity at each electrode and in each condition (attend/ignore T_1 by lag) across trials, timelocked to the onset of T_2 (*time* = 0 in the figure). The displayed N2pc difference waveforms were computed by subtracting the waveform recorded at a particular electrode ipsilateral relative to the side of the target from the waveform recorded at the corresponding electrode on the contralateral side.

Insert Figure 3 About Here

It is clear that our original supposition that the attentional blink would not influence the deployment of visuospatial attention was soundly refuted by the results. Had this hypothesis been correct, the amplitude of the N2pc would have been the same in all conditions. Clearly, this was not the case. The N2pc was largest when T_1 could be ignored (and when there was no attentional blink deficit), and smallest when T_1 had to be reported. Furthermore, when T_1 had to be reported and the T_1 - T_2 lag was short (maximum attentional blink), the N2pc was completely abolished.

A control experiment showed that the location of T_2 was well perceived despite the attentional blink, ruling out a failure of colour perception as an explanation for the results (Jolicœur et al., 2006a).

The results suggest that increasing the processing load associated with T_1 systematically reduced the differential allocation of attention to T_2 .

Spatial capture in the attentional blink paradigm.

We wondered whether the sharply-suppressed N2pc in the report- T_1 , lag 2, condition could have resulted from a failure to disengage from the central position on the screen, at the location of T_1 , rather than from interference taking place at later, central, stages of processing. We performed several experiments to address this issue. Consider first the experiment of Jolicœur, Sessa, Dell'Acqua, and Robitaille (2006b). This experiment had the same structure as the one just described, except that the colour of T_1 matched the

colour of T_2 . In the experiment just reviewed, T_1 was white and only T_2 (and the T_2 distractor) were coloured. Perhaps the reason spatial attention could not be deployed efficiently to T_2 in that experiment was that a different selection filter had to be used for T_1 and T_2 , and changing from selection on the basis of category (digit vs. letter, for T_1) to selection on the basis of colour (red vs. green, for T_2) could not be done in parallel with mechanisms that redeploy visuospatial attention.

We reasoned that colouring T_1 and T_2 in the same way would allow subjects to adopt a single selection filter to pull out T_1 and T_2 from distractors. Once a selection filter was in place, it might be possible for attention to shift to T_2 despite simultaneous processing of T_1 (despite the attentional blink) because the very same top-down selection filter could be used for T_1 and T_2 .

The results, shown in Figure 4, were clearcut: There was a large and statistically significant reduction in the amplitude of the N2pc as lag was reduced when T_1 had to be reported. Thus, despite the fact that T_1 and T_2 could be selected on the basis of colour, indeed the same colour, the attentional blink sharply attenuated the N2pc, suggesting that spatial attention could not be allocated to T_2 as efficiently during the attentional blink a few hundred milliseconds later.

Insert Figure 4 About Here

Although subjects could use colour to select T_1 , they could also use the category difference between T_1 (digit) and central stream distractors (letters). Perhaps this experiment produced similar results as the previous one because, again, different selection criteria were used for T_1 and T_2 . The results from the control condition, in which T_1 could be ignored (in principle), however, suggest that this alternative account of results is unlikely. As can be seen in Figure 4, we observed a reduction in N2pc amplitude as lag was reduced in the ignore- T_1 condition that was equivalent to the reduction observed in the report- T_1 condition. Why should this occur, if T_1 was ignored? We suppose that, in fact,

adopting a selection filter for a particular colour to select T_2 made it difficult to ignore T_1 when T_1 was also in the same colour. Indeed, accuracy of report for T_2 was about the same in the ignore- T_1 condition as in the report- T_1 condition, and exhibited a large lag effect, suggesting that T_1 could not be easily ignored, as shown in Figure 5. The fact that colour had such a powerful effect on the pattern of results in the ignore- T_1 condition (comparing across the first two experiments, Figures 2 and 5), suggests to us that it was unlikely that subjects attempted to select T_1 based on another, more complex, attribute.

Insert Figure 5 About Here

The results of the Jolicœur et al. (2006b) study, in which the attenuation of N2pc was no larger in the encode- T_1 condition than in the ignore- T_1 condition raised the possibility that the modulations of N2pc occurred mainly at the level of visuospatial attention, *per se*, rather than via mediations at later stages of processing. In the case of the experiment in which T_1 and T_2 had the same colour, perhaps the effect was mainly due to contingent capture (Folk, Leber, & Egeth, 2002; Folk, Remington, & Johnston, 1992). According to the contingent capture hypothesis, a distractor can involuntarily draw visuospatial attention to the location it occupies by virtue of a top-down attentional set to find a target with the same feature(s). Here, attention would have been captured at the location of T_1 , and remained there sufficiently long (presumably in the order of 100 ms or more) to make it difficult to redeploy attention to T_2 , to the left or right of fixation, in time to engage on T_2 before T_2 was overwritten by the T_2 mask. In the first experiment, perhaps the issue was one of a need to disengage from monitoring the central stream when T_1 had to be attended, and that monitoring activity at a particular location made it difficult to reorient attention when T_2 was presented. With a long T_1 - T_2 lag, subjects would have time to disengage from the central stream in preparation for the onset of T_2 .

Spatial attention freezes during the attentional blink.

We addressed these issues in two additional experiments involving visual stimulation for T_1 and T_2 . In the first of these, Dell'Acqua, Sessa, Jolicœur, and Robitaille (2006) presented two concurrent rapid serial visual presentation streams, one to either side of fixation, as illustrated in Figure 6. The distractors were letters. T_1 was composed of a pair of digits on 50% of trials. In the other trials, T_1 was a pair of = signs. When T_1 was composed of digits, the digits were the same on 50% of trials and different in the other trials. T_1 was then followed by a pair of letters that served as masks for the T_1 characters. After a blank interval of 50 ms, a frame including two squares, one green and one red (green and red were equated for luminance), was displayed. Each of these squares had a small gap in one randomly chosen side. T_2 was the red square for half of the subjects, and the green one for the others. The T_2 frame was followed by a pair of light grey squares with a gap on each side that served as masks (Figure 6).

Insert Figure 6 About Here

The subjects were assigned at random to one of two groups of equal size (N=15 each). Subjects in the dual-task group monitored the two concurrent rapid serial visual presentation streams of alphanumeric characters for both T_1 and T_2 . When T_1 was a pair of digits, subjects had to decide whether they were the same or different. They reported their decision at the end of the trial, without speed pressure by button press. When T_1 was a pair of = signs, they pressed the spacebar. In addition, they had to determine whether the T_2 target square had a gap in the top, bottom, left, or right side. They used keys on the numeric keypad to report the position of the gap using a spatially-compatible mapping that was learned quickly and enabled subjects to respond without looking at their fingers (and hence without moving their eyes from the fixation point) during the EEG recording session.

Subjects in the single-task group were instructed to ignore all stimuli except the T_2

square and to report the position of the gap in the target square. The same stimuli were presented to these observers as in the dual-task group, but there was no task associated with T_1 .

Each participant performed 1 block of 24 practice trials, and 8 blocks of 48 experimental trials.

Our intention was to require subjects to monitor both rapid serial visual presentation streams throughout the initial presentation up to, and including, the processing of T_1 , which required encoding and comparing two digits (one from each stream) on half of the trials (in the dual-task condition). Thus, at the time of presentation of T_2 , attention should have been spread over the two streams, in contrast to the initial attentional state in the experiments of Jolicœur, et al. (2006a, 2006b), reviewed earlier. In these earlier experiments, T_1 was presented at the center of the screen and presumably attention was focused at this location when T_1 had to be encoded or when T_1 captured attention. In the present experiment, however, it was much more likely that attention would be distributed over both peripheral locations in order to be prepared to encode the two digits in the T_1 frame (when those were presented). In the single-task condition, we suppose that attention was initially spread over the two streams in order to be able to determine as quickly as possible where to focus attention upon detection of the T_2 frame (the two coloured squares).

If the attenuation of N2pc observed in the experiments of Jolicœur et al. (2006a, 2006b) was due to a difficulty to disengage from focused attention at fixation, the results of Dell'Acqua et al. (2006) should be different, because attention was presumably distributed over the locations that would ultimately contain T_2 .

Interestingly the behavioural results for accuracy of report of T_2 exhibited a typical attentional blink pattern. Accuracy of report of T_2 (gap location in the target square) is plotted in Figure 7 for the single-task group (filled squares) and the dual-task group (unfilled circles), and for each T_1 condition (digits vs. = signs). As anticipated, the nature of the T_1 stimulus did not influence accuracy for T_2 in the single-task group, given

that T_1 could be ignored. In contrast, for the dual-task group, the task associated with T_1 caused an attentional blink and the attentional blink was larger when T_1 required encoding and comparing the symbols in the T_1 frame (to determine whether the two digits were the same or different), compared with when the symbols in T_1 simply signaled that nothing more had to be done with T_1 (i.e., when = signs were presented in the T_1 frame).

Insert Figure 7 About Here

The electrophysiological results are shown in Figure 8 (note that negative is plotted up in this figure). These are event-related potentials, timelocked to the onset of T_2 . The results were quite clear: An N2pc was found in the results of the single-task group, and this N2pc was unaffected by whether T_1 consisted of digits or = signs. The N2pc was attenuated, overall, in the dual-task group, and completely suppressed when T_1 consisted of digits (required encoding and comparison). The suppression of N2pc in the T_1 -digits dual-task condition suggests that encoding and operating on the T_1 digits prevented the differential allocation of visual spatial attention to the location of the T_2 target square. This, in turn, suggests that a substantial dual-task effect on N2pc can be observed even under conditions that were meant to encourage an initial state of divided attention. Subjects appear to have been unable to shift from an initial state in which attention was allocated equally to the two peripheral locations to a state in which attention would have been differentially allocated to the side of T_2 . Note also the very large impact of the attentional manipulations on the amplitude of the SPCN, which is largest in the single-task conditions, clearly present in the low-load dual-task condition, and completely suppressed in the high-load dual-task (T_1 -digits) condition. On the assumption that the SPCN reflects activation in visual short-term memory, the results suggest that this transfer of information into visual short-term memory was impaired by the attentional blink.

Insert Figure 8 About Here

Impaired deployment of spatial attention during the attentional blink in the absence of task switching or visual capture.

In a fourth study on N2pc and the attentional blink, Robitaille, Jolicœur, Dell'Acqua, and Sessa (2007) manipulated the relative frequency of the category into which T_1 and T_2 had to be categorized. T_1 and T_2 were squares with a gap, and the task for both targets was to decide whether the gap was in one particular side, or not (e.g., top vs. not-top). Targets with a gap at the top, bottom, left, or right, were equally likely across the test session. Consequently, a target was categorized into one of two categories that had a probability of either .25 (e.g., top) or .75 (e.g., not-top: bottom, left, or right). Previous work had shown that the attentional blink is larger and longer when T_1 is categorized into a low-frequency category than when T_1 is categorized into a high-frequency category (Crebolder, Jolicœur, & McIlwaine, 2002). This frequency effect was useful because it enabled us to manipulate the magnitude of the attentional blink effect while holding the SOA between T_1 and T_2 constant. Furthermore, we were able to create a frequency effect while presenting virtually the same stimulus (simply by moving the location of the gap in a coloured square), which equated for the relevant low-level physical characteristics of the stimulus, from a bottom-up electrophysiological point of view.

In this experiment we also ensured that the task associated with each target was the same, eliminating possible contributions of task switching to the attentional blink effects reported in the foregoing experiments (Potter, Chun, Banks, & Muckenhoupt, 1998; Visser, Bischof, & Di Lollo, 1999). The targets were red and the distractors green (equiluminant to red) for half of the subjects and this assignment was reversed for the other half. Each target frame contained two stimuli, one red and one green (a target and a distractor) both squares with a gap. The gap was never in the same location in the two squares. For the T_1 frame the squares were presented on the vertical midline, one above and one below fixation, which ensured that there were no differentially lateralized event-related potentials associated with processing T_1 . For the T_2 frame, the target and distractors were presented

one in the left and one in the right visual fields. A single, constant, T_1 – T_2 SOA of 350 ms was used.

The behavioural results showed that the relative frequency of categorization of the targets had the desired effects: a larger attentional blink when T_1 belonged to the less frequent category. The most important electrophysiological results are shown in Figure 9. Processing T_2 elicited an N2pc and the N2pc was smaller when the attentional blink was larger (namely, when T_1 was in the less frequent category). This smaller N2pc suggests that visuospatial attention could not be redeployed to T_2 as efficiently when processing T_1 produced a larger attentional blink. This result is important because the physical stimuli leading to the differential attentional blink effects on T_2 were essentially identical. Each T_1 target square was presented equally often (each with a probability of .25), but they were ultimately categorized into either a low-frequency or high-frequency category. The categorization effect, in this range of relative frequencies, has been shown to take place at a central stage of processing in the context of the psychological refractory period paradigm (i.e., additive effects of the frequency manipulation in Task₂ with SOA; Crebolder et al., 2002). Consequently, the present attenuation of the N2pc had to be due to a longer period of central processing when T_1 was categorized into the less frequent category. Importantly, T_1 and T_2 required the same processing, ensuring that the attentional blink we observed had no contributions from task switching.

Insert Figure 9 About Here

The attentional blink experiments all converge to show that visuospatial attention cannot be deployed as efficiently during the attentional blink. This conclusion may seem at odds with the view that the attentional blink results from a post-perceptual processing bottleneck relatively late in the information processing stream. Indeed, our initial expectation was that the attentional blink would not impede visuospatial attention. Nonetheless, the consistency of the finding and the sometimes impressive magnitude of the effect (com-

plete suppression of the N2pc) shows that our expectations were incorrect and points to the importance of performing experiments to test even widely and strongly held expectations.

ELECTROPHYSIOLOGICAL TESTS OF VISUOSPATIAL CAPTURE IN THE CONTINGENT CAPTURE PARADIGM.

The results of the control condition in the second attentional blink experiment, in which T_1 and T_2 had the same colour, suggested that subjects found it difficult to ignore T_1 , even when instructed to do so and when the task required only processing T_2 . In that experiment, visual capture by T_1 brought and maintained attention at fixation and thus prevented a redeployment of spatial attention to T_2 in the near periphery. We decided to devise some experiments to investigate more directly and more carefully, the notion of contingent spatial capture, using the N2pc as a measure of the locus of visuospatial attention. Attention can be guided in either a voluntary or involuntary fashion. Voluntary shifts of attention are usually driven by the goals of the individual, whereas involuntary shifts occur in response to the characteristics of the stimuli, the most salient stimuli attracting attention exogenously.

Although there is general agreement that salient visual stimuli can capture attention, there is, however, a controversy regarding the degree to which the observer's goals and search strategies can affect attentional capture. According to the contingent attentional capture hypothesis (Folk, Remington, & Johnston, 1992), a distractor can elicit an involuntary shift of attention to the location it occupies if it matches the top-down attentional control settings required to perform the task. Hence, if the task is to respond to a red target, the presentation of a concurrent red distractor will impair performance, but the presentation of a blue or yellow distractor will not (Folk, Leber, & Egeth, 2002; Folk & Remington, 1998; Lamy, Leber, & Egeth, 2004; Leblanc & Jolicœur, 2005; Serences et al., 2005). Such contingent capture effects have been observed for color, shape, movement, and sudden onset (Bacon & Egeth, 1994; Folk, Remington, & Wright, 1994). By contrast,

Theeuwes (1991, 1992, 1994, 1996) suggests that attentional capture depends solely on the sensory salience of stimuli, and that the item generating the strongest bottom-up signal within the visual display will attract attention regardless of the observer's goals. Consistent with this view, Kim and Cave (1999) observed different time courses for capture by salient stimuli and attentional shifts following top-down attentional control settings, the former happening earlier than the latter. However, these results can be explained by the adoption of a singleton search mode. When participants are forced to adopt a feature search mode in paradigms similar as the ones used by Theeuwes (1991, 1992, 1994, 1996) and Kim and Cave (1999), no attentional effects arise from the presence of salient distractors that do not match the target feature (Bacon & Egeth, 1994; Lamy, Tsal, & Egeth, 2003). Moreover, a distractor that matches the top-down attentional control settings does not have to be a singleton or create a pop-out effect within the visual search array to capture attention (Lamy et al., 2004; Leblanc & Jolicœur, 2005).

The contingent capture hypothesis states that the effect of salient distractors on behavioural performance results from a shift of visual spatial attention to the location of the distractor. However, a number of non-spatial explanations of the interference observed in capture studies have been proposed, such as filtering of the distractors (Folk & Remington, 1998; Remington, Johnston, & Yantis, 1992), delayed allocation of attention to the target (Remington et al., 2001), processing of the salient distractor (Ghorashi, Zuvic, Visser, & Di Lollo, 2003), or late selection of the target (Folk & Remington, 1998). Several behavioural studies have addressed these possibilities and yielded results consistent with this interpretation. For example, Folk and colleagues (Folk & Remington, 1998; Folk et al., 1992) have found an interaction between the distractor and the target location, responses being facilitated when the distractor preceded the target in the same location, and impaired when the target followed the distractor in a different location. Similarly, compatibility effects of the identity of the distractor on target processing have been observed, as expected if attention was focused on the distractor (Ansorge & Heumann, 2004; Remington, Folk, &

McLean, 2001; Theeuwes, 1996; Theeuwes & Burger, 1998). Finally, the time course of the contingent capture effect seems to be consistent with rapid shifts of attention to and from the location of the distractor (Leblanc & Jolicœur, 2005; Remington et al., 2001). However, overt responses depend on a wide range of processes and it is difficult to identify the stages of processing at which differences in behavioural performance arise.

The event-related potential technique, and in particular the N2pc component, provide a way to infer the locus of visuospatial attention over time as processing unfolds, and even in the absence of a response to the particular stimulus that may attract attention. In the case of attentional capture, the N2pc allowed us to monitor whether spatial attention was indeed drawn, involuntarily, to the location of a distractor that matched the target feature and whether attention was drawn to the location of equally-salient distractors that did not match the target feature.

We performed several experiments, reported by Leblanc, Prime, and Jolicœur (2007), and we summarize only one here to illustrate how the N2pc allowed us to answer an important psychological question concerning the underlying nature of contingent capture, namely whether contingent capture involved capture at a low-level of visuospatial attention, or whether the phenomenon is due to later stages of processing (e.g., late selection).

Participants performed a task similar to the one used by Leblanc and Jolicœur (2005), adapted from the study by Folk et al. (2002). In this paradigm, participants were looking for a target-coloured digit embedded in a RSVP stream of heterogeneously coloured digits. Capture was induced by presenting two irrelevant, peripheral pound signs (#) along with the digit preceding the target digit in the RSVP stream. One of the peripheral distractors was always grey. The colour of the other distractor was either the same as the target or different from the target. Leblanc and Jolicœur (2005) and Folk et al. (2002) found attentional capture — a drop in report accuracy of the identity of the target digit — when a target-coloured distractor, but not a nontarget-coloured distractor, preceded the presentation of the target. The results of Leblanc and Jolicœur (2005) are shown in

Figure 10.

Insert Figure 10 About Here

If the contingent capture effect is due to a shift of visuospatial attention to the location of the target-coloured distractor, we should observe an N2pc in response to the presentation of a target-coloured distractor, but not of a nontarget-coloured distractor. However, if the interference is due to non-spatial mechanisms, no N2pc should arise in either condition. Leblanc et al. (2007), Experiment 1, recorded EEG while subjects performed the Leblanc and Jolicœur (2005) task, simplified to include a single distractor-target SOA. The most important electrophysiological results are displayed in Figure 11. A clear N2pc was found when the coloured distractor was in the target colour but not when the coloured distractor was in a non-target colour. These results provide strong electrophysiological evidence for capture at the visuospatial level in the contingent capture phenomenon, supporting the model proposed by Folk et al. (2002). As suggested by Folk et al., the N2pc found when a distractor matched the target-defining colour shows that spatial attention was shifted to this location. The absence of an N2pc wave when the distractor was in another colour is equally important. Given the structure of the experimental design (counterbalancing of target colours across subjects, and equiluminance of the colours), the absence of N2pc for non-target coloured distractors rules out bottom-up salience of the coloured distractor as a cause of capture in this experiment (and several others reported by Leblanc et al., 2007).

Insert Figure 11 About Here

The results of Leblanc et al. (2007) provided the first electrophysiological evidence specifically implicating a shift of visuospatial attention in the contingent capture phenomenon. Other sources of interference (e.g., via late selection) could also contribute to the contingent capture effect. Indeed, Leblanc et al., Experiment 2, provided support for an interaction between early and late selection in the contingent capture paradigm. In

one condition, targets were a digit in a particular colour, among other digits (in different colours), at fixation. One of the distractors could be in the target colour or in a distractor colour. Furthermore, this distractor could be a digit (same category as the target) or a letter (different category). The other distractor was a grey letter (non-target category). The foregoing were the conditions used for half of the subjects. For the other half, the stimuli at fixation were letters the distractors were a grey digit (on one side of fixation) and either a letter (target category) or digit (non-target category), either in the target colour or in a distractor colour.

The results are summarized in Figure 12. There was no N2pc for non-target-colour distractors, despite the physical (bottom-up) equivalence of non-target colours with the target colour (indeed, despite the fact that, across observers, they were exactly the same colours). As before, there was a significant N2pc for target-colour distractors, showing that visuospatial attention had been captured by target-coloured distractors, by virtue of a match with the top-down set adopted by subjects for selection of the target at fixation. What is more, the duration of the N2pc was longer when the target-coloured symbol was in the same category as the target than when it was not in the same category as the target. The results were consistent with the notion that visuospatial attention was captured by distractors presented in the target-defining colour, and that spatial attention mechanisms took longer to disengage from this location when the category of the distractor character matched the target category than when the distractor was in a different category. See Leblanc et al. (2007) for further details.

Insert Figure 12 About Here

VISUAL SPATIAL ATTENTION DURING THE PSYCHOLOGICAL REFRACTORY PERIOD.

At the beginning of the chapter we reviewed work that examined the ability to deploy visuospatial attention during the attentional blink period. Concurrently with this work we

also examined whether the deployment of visuospatial attention would be impaired by, possibly, another type of dual-task interference, namely the interference observed during the, so-called, psychological refractory period. The psychological refractory period paradigm is the name for a class of experiments in which subjects perform two speeded responses to two stimuli (one response for each stimulus). The stimuli are usually shown sequentially and the SOA between them is varied. The typical result is that response times (RT_2) for the second target, T_2 , increase as SOA is reduced, with a slope approaching -1 at very short SOAs, while response times to T_1 , RT_1 , remain relatively flat across SOAs. This pattern of results is generally consistent with an all-or-none bottleneck model with serial response selection (see Pashler, 1994, for a review). Nonetheless, RT_1 s often also lengthen with decreasing SOA (although almost always much less than for RT_2), which is not easily accounted for by the all-or-none bottleneck model, but can be accommodated if some degree of capacity sharing can take place at central stages of processing (Navon & Miller, 2002; Tombu & Jolicœur, 2003). Recent empirical and theoretical advances in understanding dual-task interference can be found in two special issues on the topic, one edited by Band and Jolicœur (2006), and the other by Koch and Jolicœur (2006).

Brisson and Jolicœur had several reasons for examining the influence of central attention, as engaged in the psychological refractory period paradigm, and visuospatial attention. As in the attentional blink domain, there were reasons to expect that visuospatial attention would be independent from central attention. Earlier work, particularly that of Pashler (1991), suggested that the interference observed in the psychological refractory period paradigm occurred at later stages of processing relative to spatial attention (see also Johnston, McCann, & Remington, 1995). Jolicœur and colleagues (Crebolder et al., 2002; Jolicœur, 1998, 1999a, 1999b, 1999c; Jolicœur & Dell'Acqua, 1998, 1999) argued, and provided evidence, for a functional similarity between interference in the attentional blink and the psychological refractory period paradigm (see also Dell'Acqua, Jolicœur, Pesciarelli, Job, & Palomba, 2003, for electrophysiological evidence). On the other hand,

there are also differences across the paradigms in terms of masking and methods of presentation leading to differences in patterns of results that suggest that the detailed causes of observable performance in the two paradigms are often quite different. Consequently, results from the attentional blink paradigm are not necessarily predictive of results in the psychological refractory period paradigm.

Another reason to examine the N2pc in the psychological refractory period paradigm was to provide clearcut evidence for central interference on the deployment of visuospatial attention, in the absence of possible effects of visual capture by T_1 . We eliminated the possibility of visual capture by T_1 by presenting an auditory stimulus (a pure tone) for T_1 , rather than a visual stimulus, as had been the case in the attentional blink experiments.

Brisson and Jolicœur (2007b) used an auditory stimulus (pure tone) for T_1 , and simple visual forms (squares with a gap in one side) for T_2 , as illustrated in Figure 13. A speeded, four-alternative discrimination, was associated with each stimulus. For the tone, T_1 , there were four frequencies and the task was to indicate which one had been presented. For the target square (red for half of the subjects, green for the other half), the task was to indicate the location of the gap (top, bottom, left, or right). Both responses were made by button press, using four fingers of different hands for the different tasks.

Insert Figure 13 About Here

As expected, response times in Task₂, RT_2 , increased sharply as SOA was reduced, showing that the paradigm produced a large psychological refractory period effect. The main question was whether subjects would be able to deploy visuospatial attention to T_2 as efficiently during the period of dual-task interference as they can in the absence of interference. The behaviour of the N2pc component across the three SOAs can answer this question, and the results were very clear, as shown in Figure 14: The amplitude of the N2pc decreased systematically as SOA was reduced, showing that interference during the psychological refractory period impairs the ability to deploy visuospatial attention to a

lateralized visual target. Brisson and Jolicœur (2007a) showed a similar pattern of results in an experiment in which the difficulty of Task₁ was manipulated while holding the T₁-T₂ SOA constant, showing that uncertainty about the time of presentation of T₂, or overlap of the event-related components from the two stimuli, cannot explain the reduction in the amplitude of N2pc. The fact that T₁ was an auditory stimulus eliminates the possibility of visual capture by T₁ (as was possible in some, but not all, of the attentional blink experiments).

Insert Figure 14 About Here

In general, the attentional blink and psychological refractory period experiments present a rather consistent pattern of results in which the N2pc to a highly salient coloured peripheral target is systematically attenuated as dual-task interference increases. We can think of the N2pc as an electrophysiological consequence of the deployment of visual spatial attention to a particular visual target. Our results show that this consequence of attention is suppressed under high concurrent central attentional load, but they do not, yet, allow us to pinpoint how or where the interference occurs. Several control experiments have ruled out a failure of colour perception, *per se*, during the attentional blink or the psychological refractory period, as a principal cause. For the moment, we hypothesize that dual-task interference in the attentional blink and psychological refractory period paradigms originates primarily at relatively late stages of processing, such as short-term consolidation or response selection, and that these mechanisms interfere with the mechanisms that control the deployment of visuospatial attention.

ELECTROPHYSIOLOGICAL AND NEUROMAGNETIC INDICES OF VISUAL SHORT-TERM MEMORY.

Dual-task paradigms and the sustained posterior contralateral negativity (SPCN)

The experiments we described in the foregoing sections focused on visual spatial atten-

tion in dual-task and capture paradigms. As we performed them and focused on the N2pc event-related potential component, we discovered what appeared to be a second posterior contralateral negativity, often with a much longer timecourse than the N2pc. We will refer to this component as the SPCN, for sustained posterior contralateral negativity.

Similar posterior contralateral negative waves had been found in tasks requiring the encoding and retention of simple visual stimuli in reports by Klaver Talsma, Wijers, Heinze, and Mulder (1999) and Vogel and Machizawa (2004). Klaver et al. called their component the CNSW, for contralateral negative slow wave. Vogel and Machizawa (2004) called their component the CDA, for contralateral delay activity. It seems very likely that all of these contralateral negativities are closely related, and we will refer to all of them using the label SPCN because of their common sustained duration, posterior scalp and contralateral scalp distribution and sign (more negative at electrodes contralateral relative to the encoded information).

Vogel and Machizawa (2004) showed that the amplitude of the SPCN grows as the number of visual stimuli to be remembered increases, but only up to the capacity of storage in visual short-term memory (on a subject-by-subject basis). These very interesting results suggest that we can track the amount of information maintained in visual short-term memory and the timecourse of passage through visual short-term memory by measuring the amplitude of the SPCN.

Consider again the electrophysiological results of Jolicœur et al. (2006a), shown in Figure 3. Recall that these results show the contralateral minus ipsilateral difference waves relative to the side of presentation of a lateralized T_2 , in the context of an attentional blink experiment (paradigm illustrated in Figure 1). In the foregoing discussions we focused on factor effects (T_1 - T_2 SOA, and Task₁ attend vs. ignore) on the N2pc (shaded region in Figure 3). As can be seen in Figure 3, however, after the N2pc time window, the *contra* – *ipsi* difference waves for three of the four conditions all exhibit negative deflections that converge to a common amplitude of about $1.5\mu V$. Interestingly, these are the conditions for

which report accuracy of T_2 was generally high (and about equal). In contrast, accuracy in the report- T_1 condition, at lag 2, was very low, and the SPCN was essentially 0 for this condition. These results suggest to us that the SPCN was tracking the passage of T_2 into visual short-term memory. Interestingly, the onset of the SPCN appeared to be slightly earlier when T_1 could be ignored (a result which converges nicely with one we will present later in the context of the Brisson & Jolicœur, 2007b, SPCN results).

Next, consider again the results of Jolicœur et al. (2006b), shown in Figure 4. Again, the results suggest the presence of two separable components: First, an N2pc, followed by an SPCN. As in Figure 3, the pattern of amplitudes of the SPCN correlated well with the pattern of report accuracy of T_2 . In this case, T_2 could be reported well at lag 8, in both Task_1 attention conditions, and poorly at lag 2 in both Task_1 conditions. Although the SPCN was not completely abolished in the conditions with reduced T_2 report accuracy, the SPCN was significantly reduced in these conditions relative to the amplitude in conditions with high report accuracy. Furthermore, as in Figure 3, the SPCN onset appears systematically delayed when subjects had to report T_1 compared with when they could ignore T_1 .

A similar pattern of results is also apparent in Figure 8, for the results of Dell'Acqua et al. (2006). A clear SPCN was found when subjects could report T_2 with high accuracy, and the SPCN was attenuated (eliminated in this case) when report accuracy for T_2 was low.

The SPCN in Figure 9, for the results of Robitaille et al. (2007), also showed a trend in this direction, although much less so, given that the SPCN amplitude for the two Task_1 conditions converged to a common level, despite different levels of report accuracy for T_2 . Nonetheless, the initial amplitude of the SPCN (at around 380 ms), was higher when T_1 was frequent than when T_2 was rare (i.e., in the expected direction). It is possible that something about T_2 was encoded in visual short-term memory on most trials in this experiment (i.e., the fact that T_2 was a square, on a given side of fixation), but that the

location of the gap could not be extracted with equal accuracy for frequent versus rare T_1 stimuli from this representation.

The results in Figures 11 and 12, from the contingent capture experiments of Leblanc et al. (2007) are particularly interesting in the present context. In contrast with the previously considered paradigms in which subjects were actively trying to encode form information from the lateralized target, this was not the case in the capture experiments. Information at the capture location could only hinder performance in the primary task (report the identity of a letter or digit shown at fixation) and so we expect that subjects never tried to encode information at the distractor locations. It is thus most interesting that there is no obvious SPCN immediately following the N2pc waves in either of the two capture experiments summarized in Figures 11 and 12, suggesting that subjects were largely successful in not encoding information into visual short-term memory.

In the psychological refractory period experiments, subjects were trying to encode a lateralized T_2 , and generally achieved very good accuracy in all conditions (in part because T_2 was not masked, in contrast with the typical procedure in attentional blink experiments). As can be seen in Figure 14, there was a clear SPCN and the amplitude of the SPCN converged to a common voltage in all conditions, consistent with the creation of a stable and functionally equivalent trace in visual short-term memory in all conditions. Most interestingly, however, the onset latency of the SPCN was systematically delayed as T_1 – T_2 SOA was reduced. Although subjects were able to encode T_2 into visual short-term memory with equal probability at all SOAs, the delayed onset latency of the SPCN suggests strongly that it took more time to transfer a representation of T_2 into visual short-term memory when central attention was engaged on the tone (T_1). The results of Brisson and Jolicœur (2007a, 2007b) thus provided the first demonstration for delayed transfer into visual short-term memory of visual information as a result of central interference in the psychological refractory period paradigm.

Magnetoencephalographic study of the magnetic equivalent of the sustained posterior contralateral negativity (SPCN)

In the final portion of the chapter we summarize work in progress seeking convergence between electrophysiology, magnetoencephalography, and functional magnetic resonance imaging. This work involves three collaborative projects in various stages of completion, by Robitaille, Sauv e, and Jolicœur (2007), Grimault, Robitaille, Lina, Grova, Dubarry, and Jolicœur (2007), and Robitaille, Jolicœur, and Marois (2007).

Most of what we present here is based on magnetoencephalography data recorded while subjects performed a visual short-term memory task known to elicit the SPCN electrophysiological component. The aim of the work is to understand the functional and neural basis of visual short-term memory in the human brain. The paradigm used the sequence of events depicted in Figure 15. A pair of greater-than (>) or smaller-than (<) symbols was presented at the beginning of each trial. Subjects were instructed to encode information on the right of fixation following a '>' symbol and to the left following a '<' symbol. Following a blank screen (except for a fixation cross that was present throughout the trial), a set of coloured disks was presented for 200 ms. We call this display the memory array. The memory array contained either two coloured disks on each side of fixation (total of four), or four coloured disks on each side (total of eight), in colours and locations that changed randomly from trial to trial.

Insert Figure 15 About Here

There was then a 1200 ms blank retention interval. This interval was chosen to be long enough to avoid an influence of visible persistence on the memory results (Coltheart, 1980), but short enough to discourage verbal encoding (Vogel, Woodman, & Luck, 2001). Visual memory was tested by presenting a pair of disks, one on each side of fixation, each at the location of one of disks in the memory array for that trial. The task was to decide whether colour of the test disk was the same as, or different from, the colour of the disk

in the memory array at that location.

As expected, we found the expected SPCN in data from simultaneous recording of the electroencephalogram at PO7 and PO8, posterior electrode sites where the N2pc and SPCN are typically maximal (Brisson & Jolicœur, 2007a, 2007b; Klaver et al., 1999; Luck & Hillyard, 1994; McCollough, Machizawa, & Vogel, 2006; Robitaille & Jolicœur, 2006a, 2006b). We do not show these results and instead we focus on the magnetoencephalography results.

The Grand Average event-related magnetic field distribution obtained by subtracting the Grand Average magnetic field distribution observed when subjects held two objects in visual short-term memory from the distribution observed when they held four objects in visual short-term memory is shown in Figure 16. These means were computed over a time window well into the retention interval (500–1000 ms), ensuring that they reflect memory retention, rather than initial event-related responses associated with stimulus onset. The map shows the magnetic field pattern as seen from above, looking down on the sensor array, with the front of the head at the top of the figure.

Insert Figure 16 About Here

The pattern of the event-related magnetic field associated with the memory-load effect was beautifully bipolar and suggested approximately symmetric dipoles in parietal cortex. Recall, from your introductory physics course on electromagnetism, that moving charges are accompanied by a magnetic field orthogonal to the direction of current. If the current is in the direction indicated by the thumb of the right hand, the direction of the magnetic field is indicated by the direction of the curl of the fingers (the “right-hand rule”). In our lab, we also remember this relationship between the direction of the current and the lines of force of the magnetic field by imagining the direction of movement of a corkscrew as it penetrates the cork (direction of current) and the direction in which the corkscrew rotates (lines of force). In the figure, red, to yellow, to white, indicates magnetic lines of

force of increasing intensity going into the head; and blue, to turquoise, to white, indicates magnetic lines of force of increasing intensity going out of the head. An underlying current dipole is generally indicated by a pair of blue-red patches in the field map, one red patch going with one blue patch.

To interpret the distribution pattern in Figure 16, turn your right hand so the thumb points up and to the left slightly, the palm is down, and your fingers should be curling down. Now, line up your fingers with the with the red-yellow blob on the right side of the map, with your thumb pointing to the left, half way between the red and blue blobs (on the right side). Imagine that your thumb is under the figure and that your hand has freakishly long fingers that curl out of the figure at the blue blob and back into the figure at red blob (on the right), and this will give you some intuition for how to interpret this kind of magnetic field distribution map. Now, rotate your right hand so the palm is up, fingers curling up out of the head where the blue blob was found on the left side of the field map in Figure 16. You should see that you can now align this hand configuration with the blue-white and red-yellow pair of blobs on the left of the figure, indicating an underlying dipole in left hemisphere pointing up and to the right — that is, a dipole that is symmetric with the one found in the right hemisphere. Note, therefore, that the reversed red-blue patterns on the left and right sides of the map are consistent with a pair of symmetrically located and oriented dipoles, one in each hemisphere. One of the authors of this chapter confesses to some excitement when his graduate student first computed this Grand Average event-related field pattern. It was evident, at a glance, that magnetoencephalography would be an excellent tool with which to study and understand the neural basis of visual short-term memory!

Figure 17, left, shows a dipole fit solution in a model for results from a single subject in the magnetoencephalography experiment that also participated in a functional magnetic resonance imaging study involving the same task (Robitaille, Jolicœur, & Marois, 2007). We were thus able to superimpose the dipole fits on the subject's anatomical brain scan

(from the magnetic resonance imaging scan). A dipole fit model that included a single pair of symmetrically positioned dipoles, one in each hemisphere, could explain about 75% of the variance in the magnetic field map, whereas two pairs of symmetric dipoles explained about 96% of the variance. One of these pairs of dipoles was located in parietal cortex, near the border with occipital cortex, as shown in Figure 17. On the right side of the figure, we show the functional magnetic resonance imaging activation for the memory load effect, for this subject (see Todd & Marois, 2004, for details of the functional magnetic resonance imaging recording and analysis procedures used to isolate the activation shown in Figure 17). Interestingly, increasing visual short-term memory load was associated with activation of the parietal cortex, near the border with the occipital cortex.

Insert Figure 17 About Here

Our interpretation of the dipolar field pattern on each side of the Grand Average field map is supported by infomax independent components analysis of the magnetoencephalography data. Independent components analysis refers a family of “source separation” algorithms that decompose multisensor data into a linear combination of independent sources, called components. Typically independent components analysis algorithms separate components that are completely independent of each other: activity in one source only randomly predicts activity in any other (Cichocki & Amari, 2002). We used infomax independent components analysis, which maximizes the independence (information) of each component without enforcing complete independence — a more physiologically realistic assumption (Makeig et al., 1996). Each component comprises a distribution across sensors (a spatial map), and a single waveform showing how the amplitude of that source changes over time. The independent components analysis decomposition is perfect: the original data can be perfectly reconstructed by recombining activity of all the components. Infomax independent components analysis assumes that the actual sources generating the data are spatially stable (the brain does not move relative to the magnetoencephalograph

sensors) and combine linearly (magnetic field do) — but the method makes no a priori assumptions concerning experimental conditions or brain structures, and is thus a form of “blind source separation” (Makeig et al., 1997). In physiological terms, if the amplitude of a neural source changes over time independently of other sources at other locations, independent components analysis should isolate each source’s particular magnetic pattern across the 275 magnetoencephalograph sensors.

We performed infomax independent components analysis on the data from subjects in the magnetoencephalography experiment using the paradigm outlined in Figure 15. Each subject’s data is analysed separately because, even if there was a common neural generator subsuming a psychological function (such as visual short-term memory) across subjects, it cannot be assumed that this source will be in exactly the same orientation and position in each subject, relative to the sensor array (because of anatomical differences from one brain to the next and because of differences in the position of the head relative to the sensors. Nonetheless, we found components in several individuals that are very similarity in their spatial field distribution.

Figure 18 shows selected components from the independent components analysis results for nine subjects. Some of these components are remarkably similar across subjects. For example, compare the components shown for subjects 2, 13, and 21, which have similar spatial structures; also compare those for subjects 5, 18, and (to a lesser extent) 20. We also show a number of other components, from other subjects, that have well-defined and simple spatial structure. Some components appear to reflect source in left hemisphere, whereas others are for a source in right hemisphere, converging with the evidence from functional magnetic resonance imaging and event-related potentials suggesting that visual short-term memory engages neural activity in both hemispheres.

Insert Figure 18 About Here

Each component isolated by independent components analysis has an associated ac-

tivation timecourse. We performed a separate event-related average of these timecourses for trials in which there were two items in memory and for trials in which there were four items in memory. Figure 19 shows these event-related averages for the activation patterns associate with the components shown in Figure 18. All of these components show differential activity levels during the retention interval for trials with different memory loads. This is not entirely surprising because this was one of our criteria for selecting these particular components. The vast majority of components have activation profiles that do not show this effect. Nonetheless, it is most interesting that the independent components analysis allowed us to extract components that appear to reflect neural activity specifically related to the maintenance of information in visual short-term memory.

Insert Figure 19 About Here

Dipole fits were computed for the independent components analysis spatial maps shown in Figure 18. The results are shown in Figure 20. As would be expected from the similarity of some of these component spatial maps, their associated equivalent current dipoles tended to cluster. Interestingly, many of the dipoles were in the posterior parietal region in the same general region found by Todd and Marois (2004) in a functional magnetic resonance imaging experiment designed to discover the neural locus of retention in visual short-term memory (see also Figure 17). We also included two components with activity profiles suggesting a participation in visual short-term memory (a clear load effect in the component activation timecourses), which did not localize in the same regions. These dipoles are shown in blue in Figure 20. One of them was clearly more medial than the others (in red), and the other was clearly lower and more lateral. The independent components analysis results suggest that the posterior parietal region contributes to the observed event-related magnetoencephalography results shown in Figure 16, but that other regions also participate in a broader network involved in retention in visual short-term memory.

Insert Figure 20 About Here

Source localization of the neural generagors of induced activity during visual short-term memory retention.

In this final section we summarize analyses of induced activity discovered in time-frequency analyses of magnetoencephalography recordings made while subjects performed the visual memory task illustrated in Figure 15. We subjected trial-by-trial data, in each of 271 channels of data, to wavelet analysis and plotted power, at different frequencies, over time. The time-frequency maps were computed for 11 subjects for which the data were sufficiently well-behaved. We found that power at about 10–12 Hz (in the so-called α -band) tended to increase just before the onset of the to-be-encoded memory array, then to decrease sharply, followed by a large increase in power during the retention interval (roughly from 600 to 1400 ms). We quantified these patterns by computing the average power, in 1 Hz intervals at each moment during a 500 ms pre-memory array interval and used the mean and standard deviation of the baseline power to compute a z-score for the power observed in a window of -500 to +1400 ms relative to the onset of the memory array. For each subject, and each memory load condition (encode left load 2; encode right load 2; encode left load 4, encode right load 4), we found the magnetoencephalography sensor over the hemisphere contralateral to the encoded coloured disks that had the maximum mean power in the α -band, in a window of 600–1400 ms. We then averaged the z-score maps across subjects and also computed difference maps by subtracting the z-score map for load-2 trials from the map for load-4 trials, for each encoding side (encode left vs. encode right). The resulting z-score time-frequency map for encode-right trials (sensors over left hemisphere) is shown in Figures 21. The results for encode-left trials essentially the same.

Insert Figure 21 About Here

It is evident in Figure 21 that the α -band power during the retention interval is significantly larger for load-4 trials than for load-2 trials, demonstrating that our visual short-term memory load manipulation caused significant changes in induced brain oscillatory activity during the retention interval. Interestingly, these changes in neural oscillations are not visible in the event-related averages because of variations in the phase of the oscillations relative to the onset of the memory array (Tallon-Baudry, Bertrand, Peronnet, & Pernier, 1998).

The trial-by-trial phase vectors were averaged for each condition (left-2, right-2, left-4, right-4), averaged over trials, subjects, and then subtracted (right-4 minus right-2; left-4 minus left-2). In Figure 22, we show the load-4 right minus load-2 right difference in degree of phase locking. Soon after the onset of the memory array, there is a greater increase in phase-locked activity for load-4 trials than for load-2 trials, probably reflecting a larger event-related response when there were more disks in the visual display. There were no obvious difference in trial-by-trial phase locking during the retention interval, where we found the greatest change in alpha-band power related to memory retention. This pattern of results was the same for the pre-subtraction phase maps for each load condition.

The results shown in Figures 22 and 23 highlight the importance of looking at induced activity (caused by the stimulus, but not phase-locked with the stimulus) in addition to looking at event-related averages (evoked, or phase-locked, activity). Tallon-Baudry et al. (1998), reported significant increases in γ -band (20–80 Hz) power during retention in visual short-term memory. Our experiment was not ideally designed to observe γ -band activity because our sampling rate was only 240 Hz (imposing a low-pass filter at acquisition at 60 Hz, which may have attenuated induced γ). Although there are hints of changes in power, related to memory load, at about 20 Hz, and perhaps at 35 Hz (Figure 22), it is clear that these effects are much smaller than the changes in power in the 10–12 Hz region. In a more recent experiment, we sampled magnetic activity at 600 Hz to ensure that γ -band activity would not be attenuated by filtering. Again the most prominent effects on induced

power were in the α -band. It is possible that induced γ may be stronger for memory for visual shape (Tallon-Baudry et al., 1998; Tallon-Baudry, Kreiter, & Bertrand, 1999), than for memory for colour (present work). We will address this interesting possibility in future research.

Insert Figure 22 About Here

For the moment, it is clear from our results that visual short-term memory for coloured disks caused induced activity mainly in the α -band. In order to determine the neural sources of this memory-related activity, we computed the average power in a window from 500 ms to 1200 ms post memory array onset, in the α -band, for each sensor, and we created a sensor map of the resulting values, which is shown in Figure 23, for one observer (for whom we had a structural magnetic resonance image of the brain), for one condition (load-4 right). Most interestingly, the distribution of α -power had two clear peaks at posterior sensors over occipito-parietal cortex. Similar distributions were found in maps for the other conditions (with varying amplitudes), for each of the four subjects in our analyses (the four for whom we had a structural magnetic resonance image).

Insert Figure 23 About Here

The very similar bilateral posterior distribution of memory-related α -power across conditions and subjects encouraged us to develop a method to find the neural sources of this activity. Existing source localization techniques could not be used, however, because the mathematics of the forward solution (computing the expected sensor activity given a known source) used to compute solutions to the inverse problem (inferring sources given an observed pattern of activity at the sensors) have been worked out for linear models, and power is a non-linear value. Grimault et al. (2007) devised way around this problem. For each trial, the time of peak activity in the α -band, in the retention interval (500–1200 ms), was found, for a given sensor (called the reference sensor, chosen to be in the

zone of maximum power in the map of power distribution, Figure 23). This time defined an event of interest that was later used to compute a new event-related average of the original magnetoencephalography signals. In other words, we shifted the signals, trial by trial, so as to align the moment of peak activity in the frequency of interest across all trials. We shifted the signals from all other sensors using the event time stamps from the reference sensor, and we averaged the signals using this new event-related alignment. This event related average, like any other event related average, is in the original metric of the data, and could thus be localized with existing source localization methods.

Because the method aligns the data from all sensors based on events defined for the reference sensor, averages for other sensors reflect the degree to which α -power is phase-locked with α at the reference sensor. The method revealed strong phase synchrony among sensors close to the reference sensor, which is not very surprising; but also for sensors near the α peak over the opposite hemisphere. These results suggest that cortical regions in the two hemispheres responding to load in visual short-term memory likely participate in a bilateral neural network. We are actively pursuing these very interesting preliminary findings.

Figure 24 shows the sensor map of the intensity of the aligned α -band signals for the encode-4 right condition. The map shows a nice peak at posterior sensors that are out-of-phase for left versus right sensors.

Insert Figure 24 About Here

Figure 25 shows the results of distributed source localization of induced peak *alpha* activity, during the retention interval, using the method of maximum entropy of the mean (Grova et al.), for the activations computed using the method of Grimault et al. described above (Figure 23). This distributed source localization method constrains the inverse solution using a reconstruction of the cortical surface of each observer, extracted from their anatomical magnetic resonance imaging scan. A strong peak in the occipito-parietal

gyrus was found, providing very good convergence with other indications that this region appears to play an important role in the maintenance of information in visual short-term memory.

Insert Figure 25 About Here

SUMMARY AND CONCLUSIONS

By making use of recent advances in electrophysiology, magnetoencephalography, and functional magnetic resonance imaging, gained a better understanding of the functional and neural basis of visuospatial attention and visual short-term memory. Our research team combined recordings of the electroencephalogram and the ERP technique, with several dual-task paradigms. We focused on a component of the ERP called the N2pc and used it to track the efficiency and timecourse of the deployment of visuospatial attention. We discovered that the deployment of visuospatial attention is less efficient, and sometimes appears to be severely impaired, during concurrent central processing. This was true both for the attentional blink paradigm, using unimodal visual stimuli, and for the psychological refractory period paradigm, using crossmodal auditory-visual stimuli. The N2pc ERP component, a moment-to-moment index of the deployment of visuospatial attention, was attenuated or abolished, under concurrent central processing load.

Overall, the results suggest that the control of visuospatial attention depends on mechanisms that overlap with central bottleneck mechanisms implicated in the attentional blink and psychological refractory period paradigms. Interestingly, these are results that were not originally anticipated given the belief that spatial attention is a relatively early mechanisms whereas dual-task bottlenecks involve relatively late central processing mechanisms (such as response selection or short-term consolidation in working memory systems).

Electrophysiology in the context of contingent capture experiments enabled us to show that contingent capture is accompanied by a significant N2pc wave. This result provides strong evidence for capture at the level of visuospatial attention (as opposed

to later stages of processing). Interestingly, in these studies, the later SPCN (sustained posterior contralateral negativity) wave was not evident. In contrast, in tasks in which subjects actively try to process peripheral targets, we typically observe both an N2pc and an SPCN.

While the N2pc appears to track the locus of visuospatial attention, the SPCN appears to track encoding and retention in visual short-term memory. The fact that there is no SPCN in the capture experiments and significant SPCNs when peripheral stimuli are targets suggests that subjects have good control over what enters and what does not enter visual short-term memory. Indeed, one of the paradigms used to study visual short-term memory, illustrated in Figure 15, critically hinges on the ability to select information on one side of fixation, at the expense of information on the other side. In most experiments, the amplitude of the SPCN provided a very good correlate of report accuracy for the target(s) giving rise to the SPCN, reinforcing our interpretation that the SPCN reflects passage through visual short-term memory, and that encoding in visual short-term memory may be necessary for conscious report.

In the final portion of the chapter we summarized recent magnetoencephalography results that focused on understanding the neural basis of visual short-term memory. This is work in progress and we may have raised more questions than we provided answers. Nevertheless, we are strongly encouraged by our preliminary results, based on analyses of evoked and induced activity, and on the exciting prospects for convergence across different neuroimaging techniques. Although it is likely that multiple areas in the brain contribute to visual short-term memory, it appears that there is a particularly important node in this network located in parietal cortex, at the border with occipital cortex.

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Figure Captions

Figure 1. Modified attentional blink paradigm used in the experiment of Jolicœur, Sessa, Dell'Acqua, and Robitaille (2006a). T_1 was a white digit presented at the center, followed by 1 distractor. T_2 was red (half of the subjects) or green, presented 3° to the left or right of fixation, and followed by a pattern mask. T_1 was followed by 1 letter at fixation in the lag 2 condition (shown here) and by 7 letters in the lag 8 condition (not shown).

Figure 2. Proportion correct report of T_2 , for each lag, in the ignore- T_1 and the report- T_1 conditions in the experiment of Jolicœur, Sessa, Dell'Acqua, and Robitaille (2006a).

Figure 3. Contralateral minus ipsilateral difference waves used to isolate the N2pc and the SPCN (sustained posterior contralateral negativity), at electrode site T5/T6, for the 4 conditions in the experiment of Jolicœur, Sessa, Dell'Acqua, and Robitaille (2006a). The shaded region shows the time window used to quantify the N2pc.

Figure 4. Electrophysiological results from the experiment of Jolicœur, Sessa, Dell'Acqua, and Robitaille (2006b). Contralateral minus ipsilateral difference waves for the T5/T6 electrode pair, for each condition (ignore- T_1 vs. report- T_1 , at lags 2 vs. 8). The N2pc component is visible in the 160–270 ms time window. Note the second sustained posterior contralateral negativity (SPCN) observed from 300–500 ms.

Figure 5. Proportion correct report of T_2 (contingent on correct report of T_1 in the report- T_1 condition), for each condition (ignore- T_1 vs. report- T_1) and each lag (2 vs. 8) in the experiment of Jolicœur, Sessa, Dell'Acqua, and Robitaille (2006b).

Figure 6. Stimulus events in each trial of the experiment of Dell'Acqua, Sessa, Jolicœur, and Robitaille (2006). The squares of in the T_2 frame were red and green in the actual experiment (shading was used here for illustrative purposes).

Figure 7. Mean percent correct report of the location of the gap in T_2 in the experiment of Dell'Acqua, Sessa, Jolicœur, and Robitaille (2006).

Figure 8. Electrophysiological results in the experiment of Dell'Acqua, Sessa, Jolicœur, and Robitaille (2006). The contralateral response is plotted using a dashed line and the ipsilateral response is plotted using a solid line. Note that positive is plotted down.

Figure 9. Electrophysiological results in the experiment of Robitaille, Jolicœur, Dell'Acqua, and Sessa (2007). Event-related difference waves, contralateral minus ipsilateral, relative to the side of presentation of T_2 , timelocked to T_2 onset, for frequent and infrequent T_1 targets.

Figure 10. Results of Leblanc and Jolicœur (2005). Percent correct report of the identity of a coloured digit presented at fixation in a rapid serial visual presentation stream of digits in other colours, as a function of the colour of the two lateralized distractors, and of the distractors-target SOA. The distractors could both be grey; one grey and the other in the target colour; one grey and the other in a non-target colour.

Figure 11. Results of Leblanc, Prime, and Jolicœur (2007), Experiment 1. Electrophysiological, event-related difference waves, contralateral minus ipsilateral, relative to the side of presentation of the coloured distractor, timelocked with the onset of the distractor frame, as a function of the colour of the lateralized distractors.

Figure 12. Results of Leblanc, Prime, and Jolicœur (2007), Experiment 2. Electrophysiological, event-related difference waves, contralateral minus ipsilateral, relative to the side of presentation of the coloured distractor, timelocked with the onset of the distractor frame. The labels show the possible content of a distractor frame (just prior to the target digit) for a subject searching for a blue digit in the central rapid serial visual presentation stream. A blue digit distractor is thus a target-colour distractor in the target category (blue waveform), a blue letter is a target-colour distractor in the non-target category (yellow waveform). Notice the N2pc for these conditions, and the larger and longer N2pc for the target-colour, target-category, distractor (blue waveform). Peripheral distractors in other colours would be in non-target colours for this subject (green and orange waveforms), for which N2pc amplitude was not statistically

different from zero.

Figure 13. Sequence of events in the experiment of Brisson and Jolicœur (2007b). The red and green squares in the visual display had the same luminance to equate bottom-up sensory responses.

Figure 14. Electrophysiological results in the experiment of Brisson and Jolicœur (2007b). The waveforms show the difference between contralateral and ipsilateral waveforms, pooled across three posterior electrode sites near the peak of the N2pc wave. In the N2pc time window (180–260 ms) the amplitude of the contralateral negativity was maximal for long-SOA trials (1000 ms SOA) and it decreased sharply as SOA was reduced. Note the later sustained posterior contralateral negativity (SPCN), which eventually reached the same amplitude in all SOA conditions, but with an onset that was delayed as SOA was reduced.

Figure 15. Sequence of events in the experiment of Robitaille, Sauv e, and Jolicœur (2007).

Figure 16. Grand Average event-related magnetic field distribution obtained by subtracting the average magnetic field distribution observed when subjects held two objects in visual short-term memory from the distribution observed when they held four objects in visual short-term memory, in the experiment of Robitaille, Sauv e, and Jolicœur (2007). The averages were taken over a wide time window during the retention interval (500–1000 ms). Blue indicates an outward field, red inward.

Figure 17. Results from a single observer in an unpublished study by Robitaille, Marois, and Jolicœur, using the paradigm illustrated in Figure 15. On the left we show a dipole fit analysis for magnetoencephalography results using a pair of symmetric dipoles fit to the memory load effect illustrated in Figure 16. On the right we show that, as in the study of Todd and Marois (2004), increasing the load in visual short-term memory produces a BOLD response activation peak at the border between occipital and parietal cortex when the same subject was tested using fMRI using a close variant

of the paradigm (adapted for fMRI testing). Note that one of the dipole pairs in the magnetoencephalography results was localized in the same region as the fMRI activation peak, suggesting that the two methods converge nicely in suggesting that a region in the occipito-parietal border plays a special role in the retention of information in visual short-term memory.

Figure 18. Magnetic field across 275 sensors for the parietal component exhibiting a large memory load difference extracted from the independent components analysis in each of nine subjects. Red indicates an outward magnetic field, blue inward. Most subjects exhibit a dipolar field over parietal cortex indicating an upward-oriented current located midway between the maximum outgoing sensor (diamond) and maximum incoming sensor (darkest blue). This dipolar pattern occurred in the left hemisphere in some subjects (sj5, sj18) and the right hemisphere (sj13, sj21) in others. Some subjects (sj2, sj12) exhibit an apparent mixture of parietal sources in two hemispheres. In other subjects (sj20, sj27) the parietal source maximally sensitive to load was located more posteriorly. Most of these subjects had several other dipolar components in other areas that also exhibited load differences. Top sensors cover anterior cortex, left is left. The diamond denotes the maximal positive sensor (whose time course is shown in the next figure).

Figure 19. Waveforms of independent components exhibit large amplitude responses during retention of 4 objects versus 2 objects. All subjects but one show activation in both memory load conditions, however retention of 4 objects results in higher amplitude activation of this source specifically during the retention period, where the differences in mean amplitude (500–1400 ms) were significant (in a within-subjects t-test over trials) for all these subjects; $p < .001$ for all subjects except Subject 27. Note also the sharp wave preceding and following the memory retention period, which may indicate the arrival of visual information into this parietal source. The first sharp wave (at about 100–200 ms) does not show large memory-load differences, while the latter one

does (at about 1800 ms). These activation patterns suggest that the parietal source maintains visual information during the retention interval.

Figure 20. Dipole localizations of parietal independent components show many similarly oriented sources in parietal cortex. Red dipoles indicate sources located clearly within parietal cortex. Blue dipoles indicate sources in other areas: one is relatively medial and posterior (sj27), the other is relatively lateral, anterior and inferior (sj19). The most anterior left hemisphere dipole location is similar to those on the right, with an opposite (mirror) orientation. The mean goodness-of-fit of the red dipoles was 90.1%. The mean Talairach coordinates for the red dipoles is X 27.1, Y -46.04, Z 50.0, after all the X axis (left-right) values are made positive for averaging.

Figure 21. Results of time-frequency analysis (z-score relative to pre-stimulus baseline; averaged over eleven subjects) for the contralateral sensor with the largest power in the alpha band, during the retention interval. This map shows the difference in z-score for the load-4 condition and the load-2 condition. Frequency is plotted on the ordinate, time (in seconds) on the abscissa. The colour in the graph indicates the value of the z-score at that frequency and time. Note the large yellow-red band at about 10 Hz, from 500–1400 ms that indicates that α -band power increased significantly during the retention interval as memory load increased.

Figure 22. Differences in trial-by-trial phase locking across the load-4 encode right condition and the load-2 encode right condition. Time (in seconds) is on the abscissa and frequency on the ordinate. The colour in the figure codes the degree to which an occurs at the same relative phase from one trial to the next. In this difference map, we examined how trial-by-trial phase locking varied across memory loads. There was greater phase locking in load-4 trials than load-2 trials, but only immediately after the onset of the memory array, probably indicating a greater event-related response in load-4 trials.

Figure 23. Sensor distribution of the power in the alpha band during the retention interval

(500–1200 ms) based on time-frequency analysis, for one observer, in the load-4, right, condition.

Figure 24. Sensor map of aligned α -band signal amplitude, using a sensor over left hemisphere as the reference sensor. This map shows a strong peak over left hemisphere, indicating phase-locked activity, and a peak over right hemisphere, also indicating phase-locked activity (relative to the reference sensor), but also indicating a significant phase shift (indicated by the change in sign of the induced activity).

Figure 25. Source localization of induced activity in the alpha band, using the method of maximum entropy on the mean (Grova et al.), using the method developed by Grimault et al. (2007). The reconstructed surface at the border between grey and white matter was used to constrain the inverse problem. Note the peaks at on the occipito-parietal girus, at the border between parietal and occipital cortex.

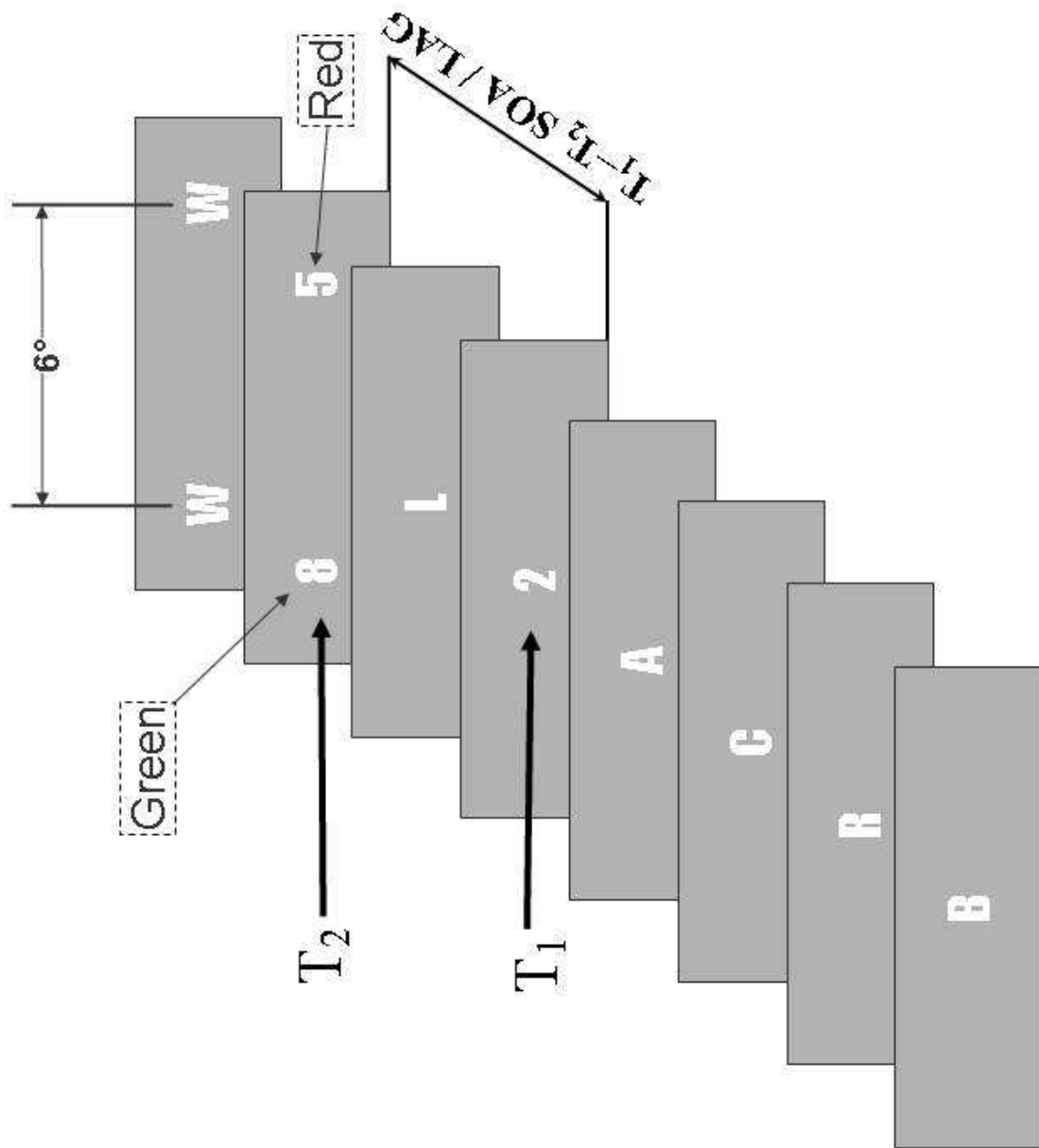


Figure 1

Figure 1

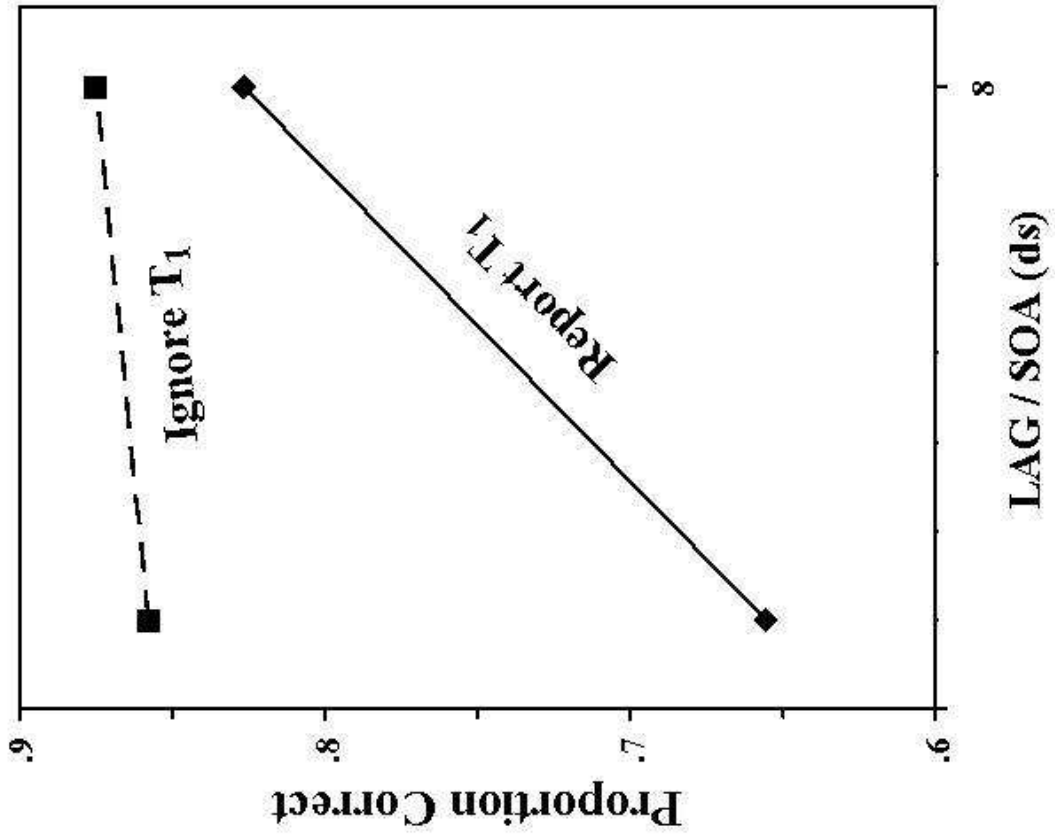


Figure 2

Figure 2

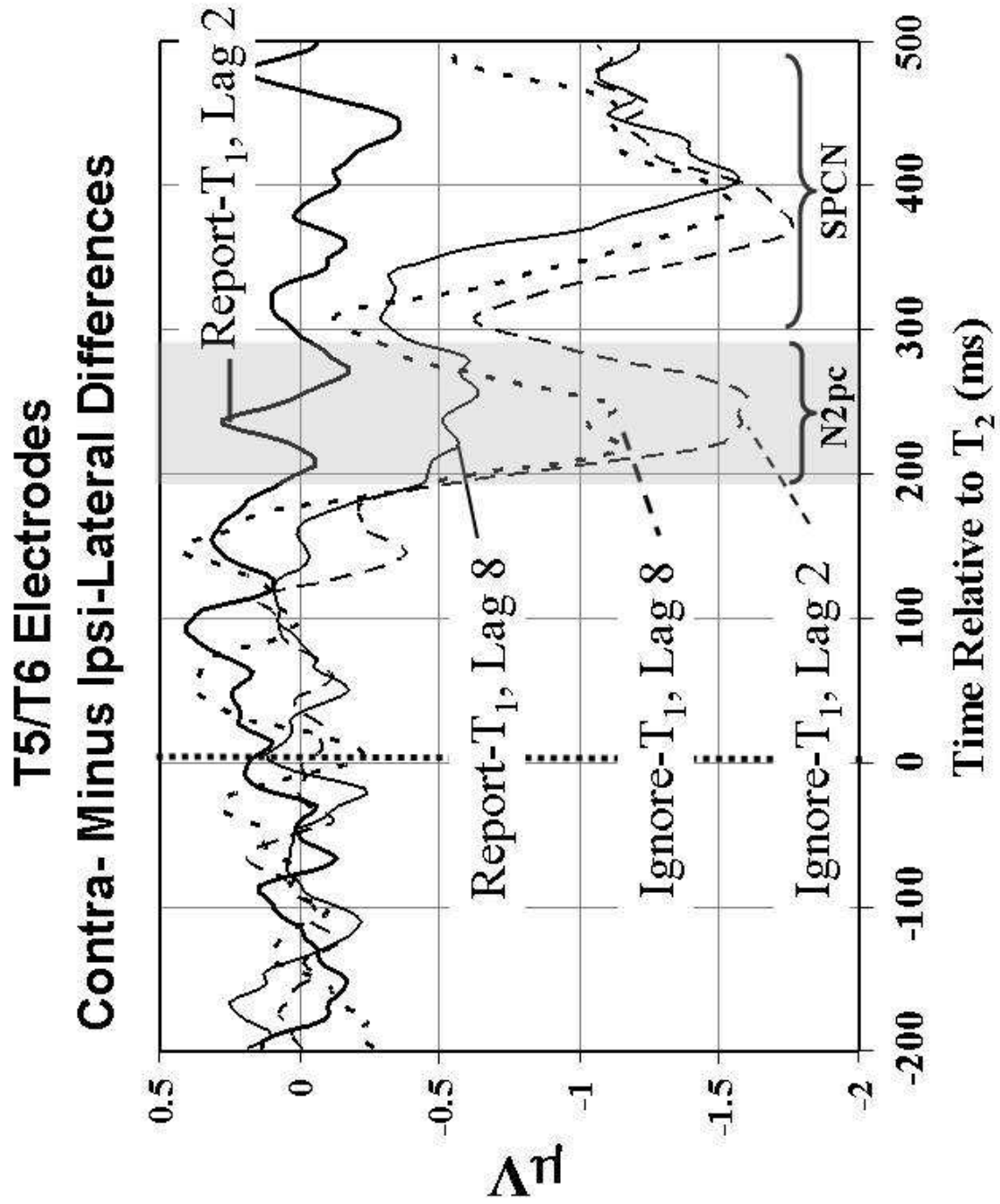


Figure 4

Figure 3

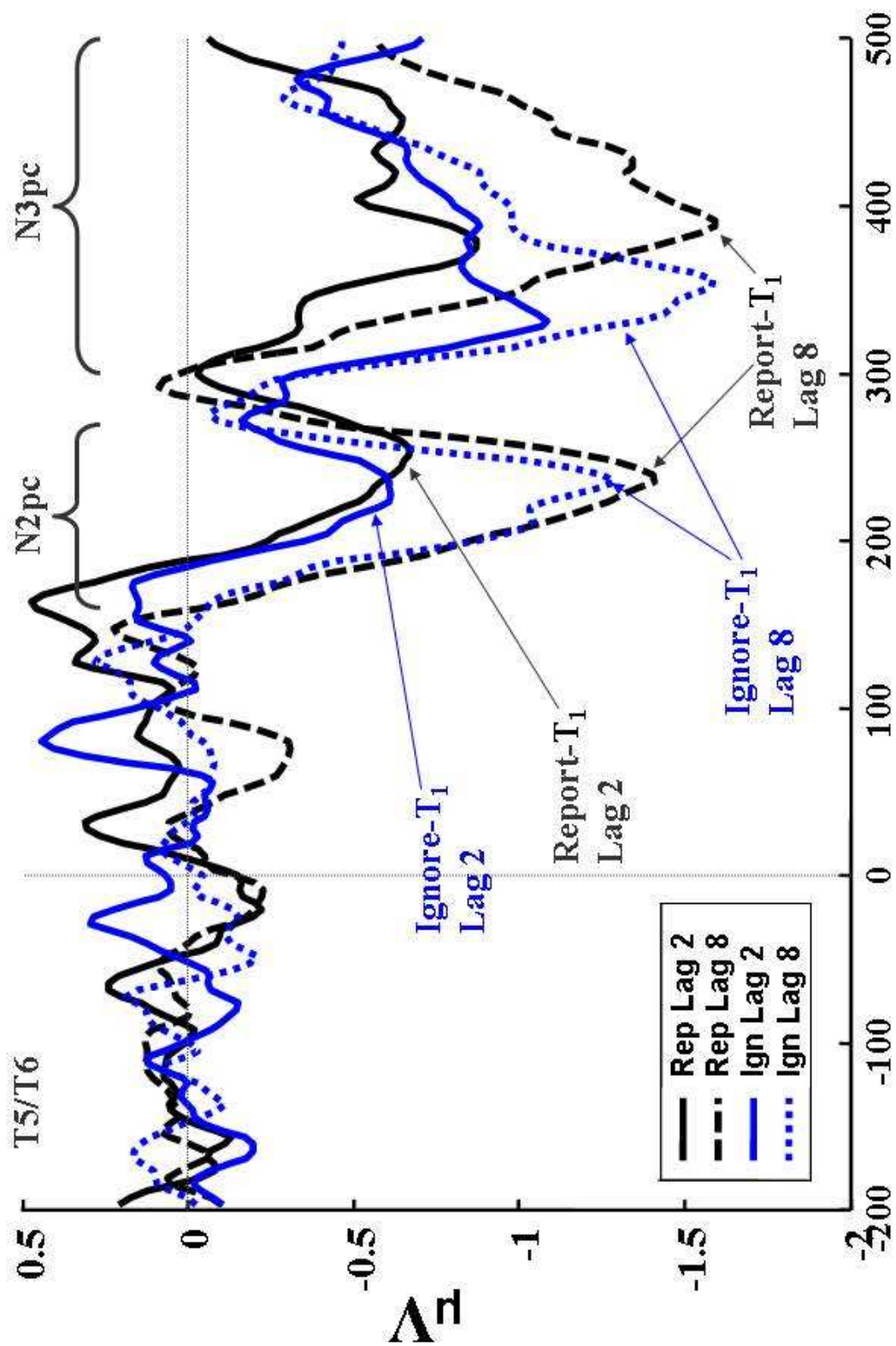


Figure 3

Figure 4

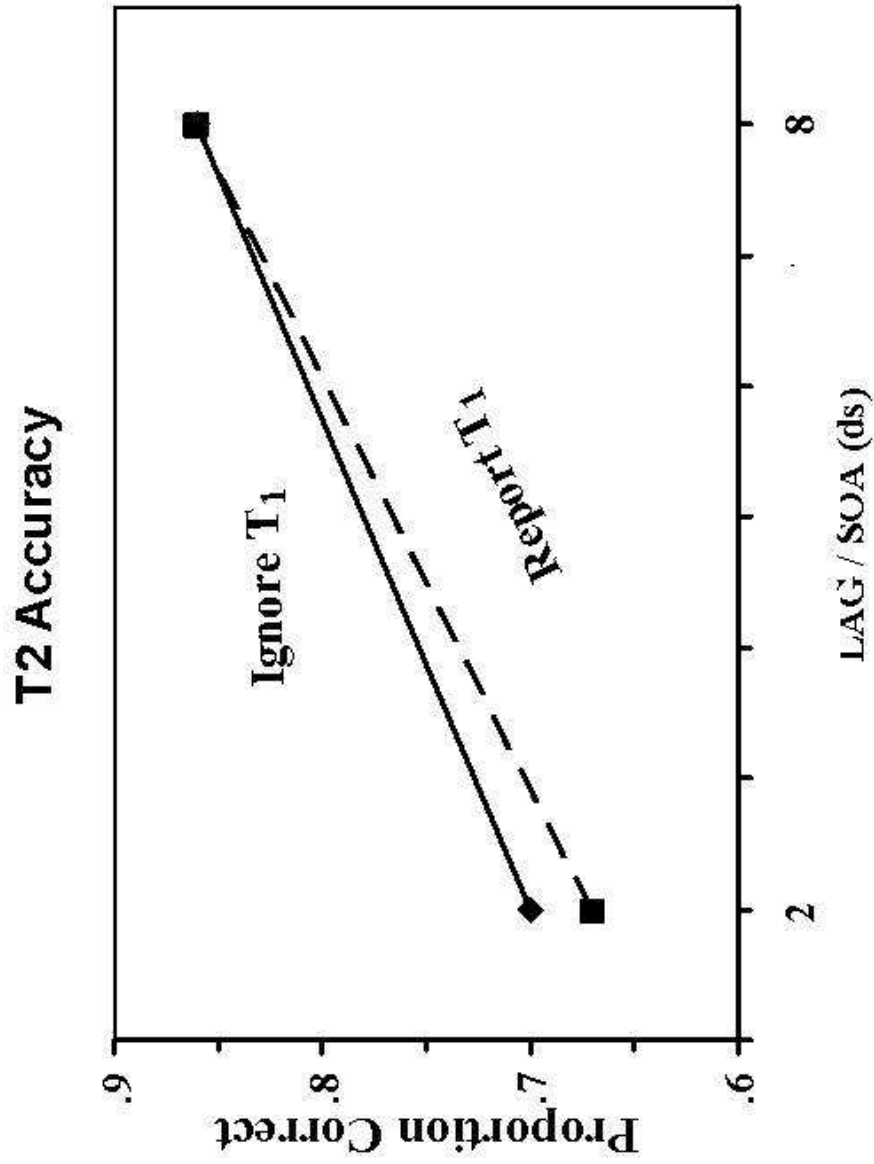


Figure 2

Figure 5

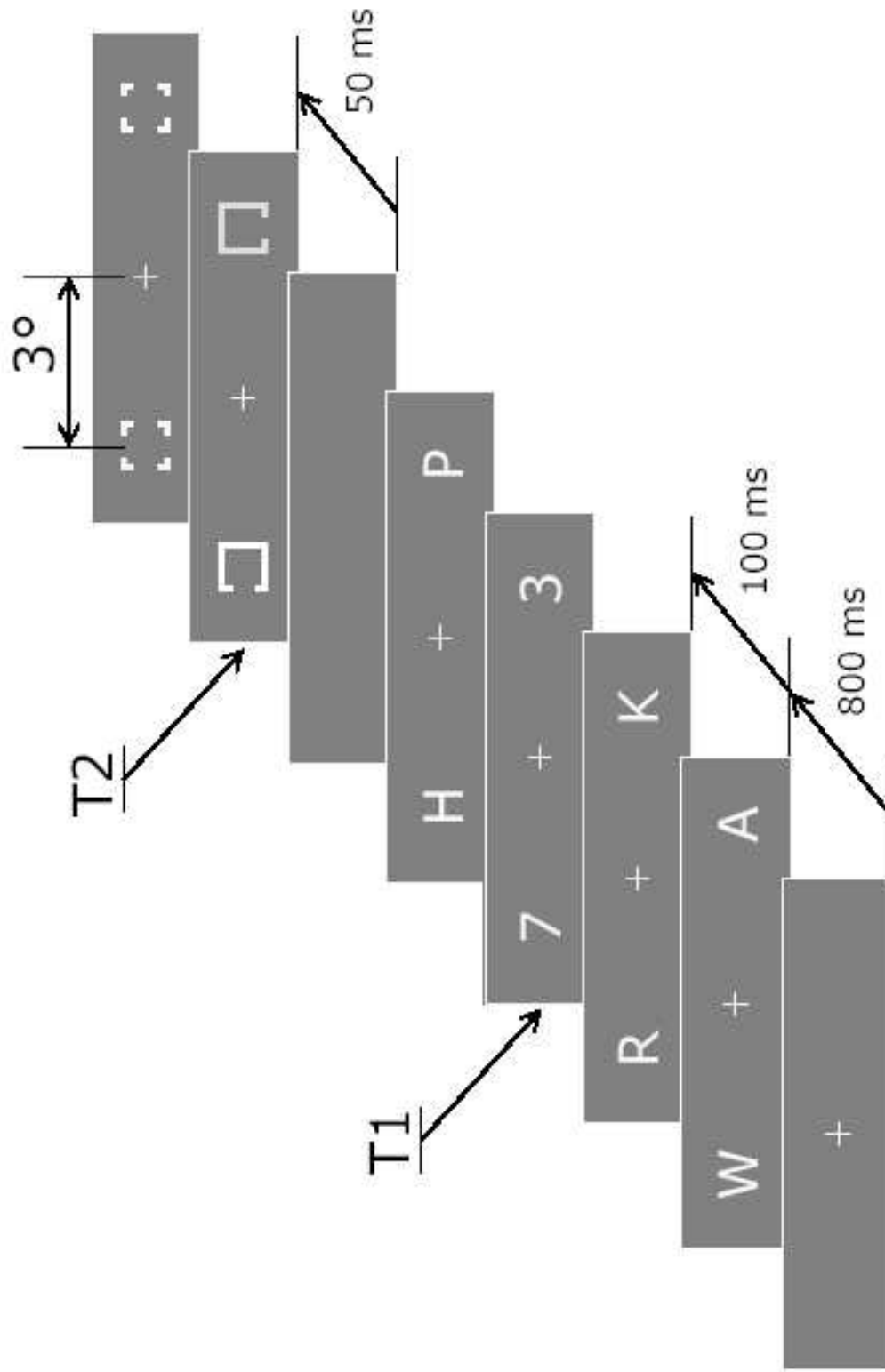


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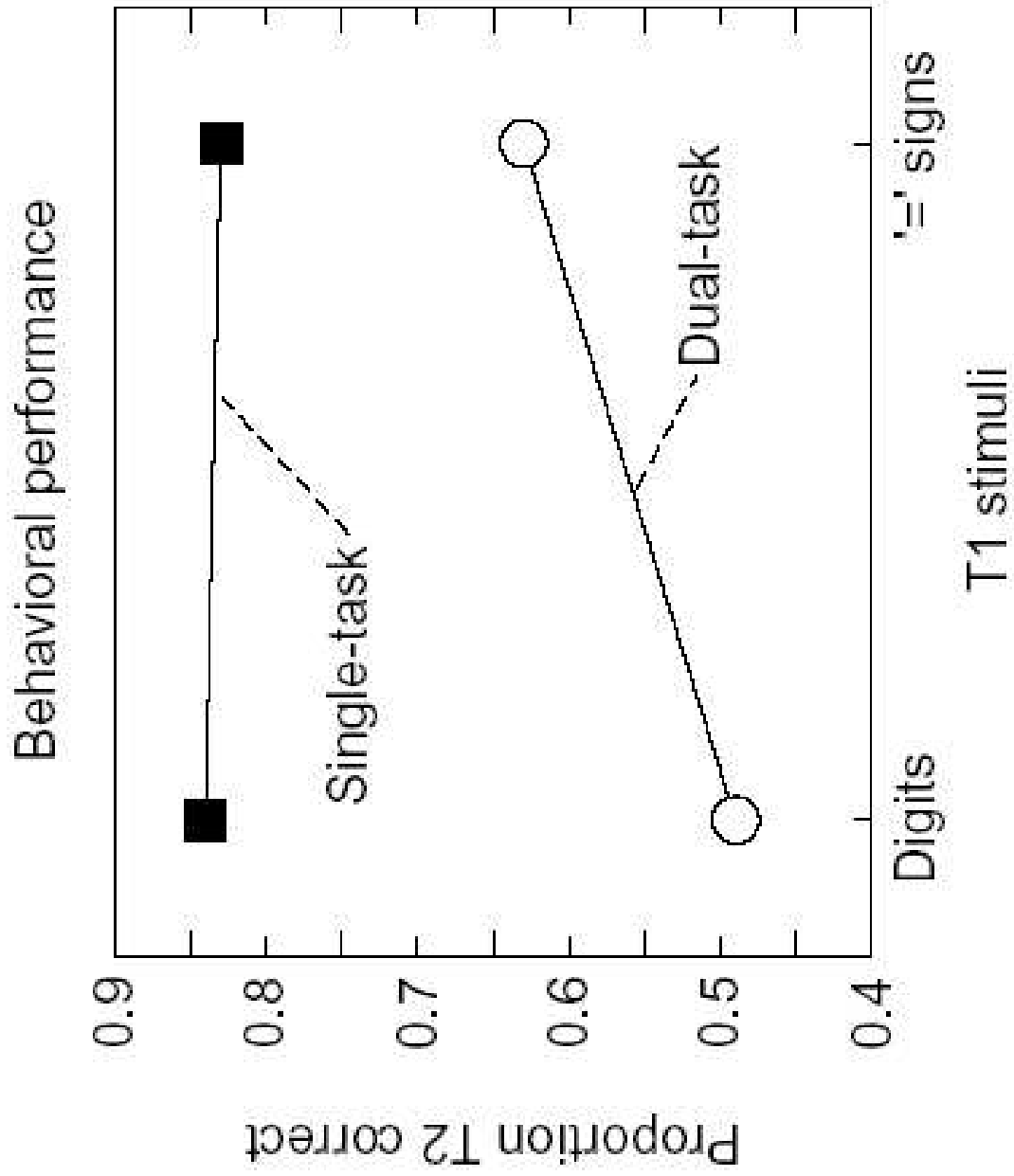


Figure 7

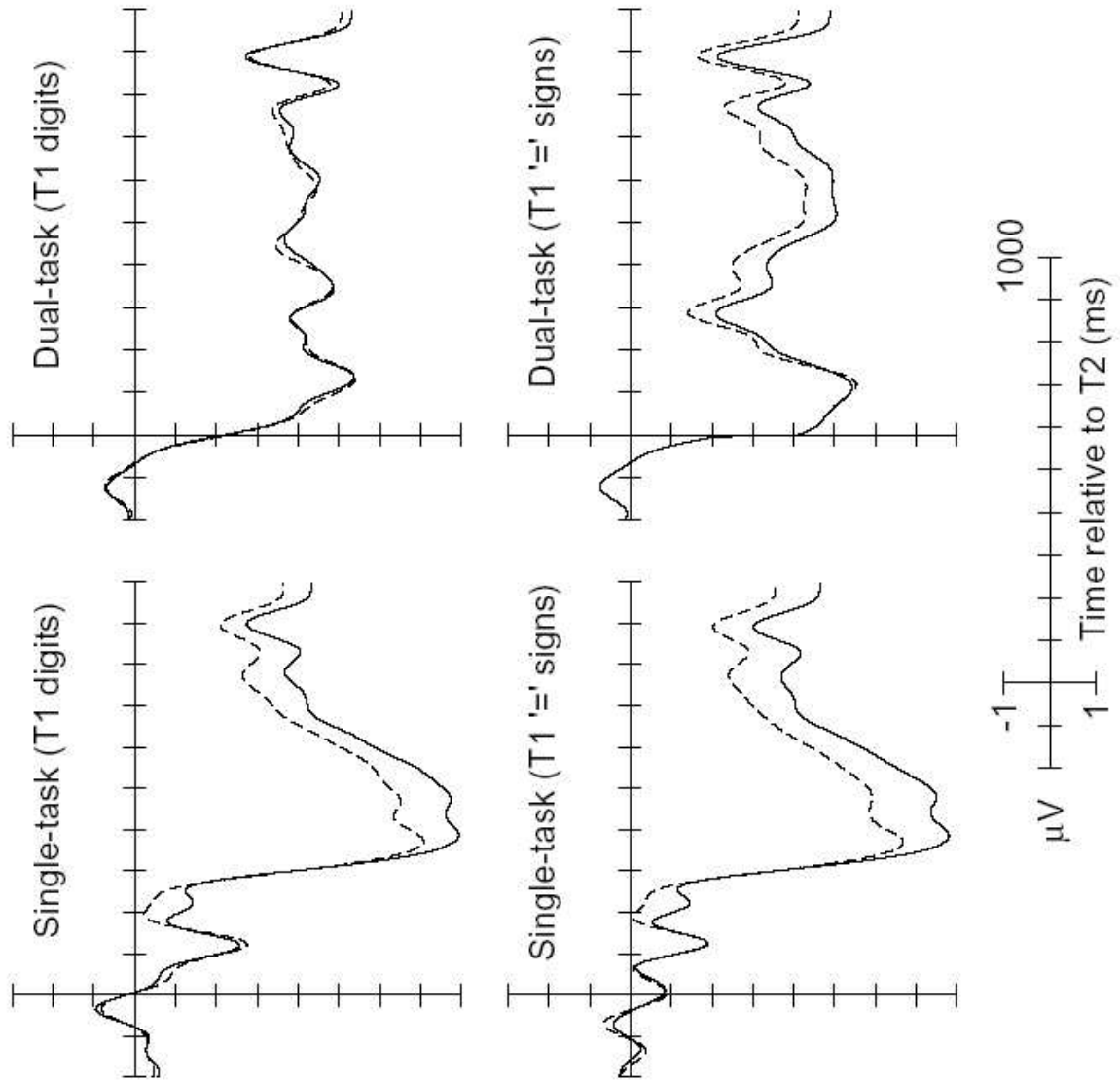


Figure 8

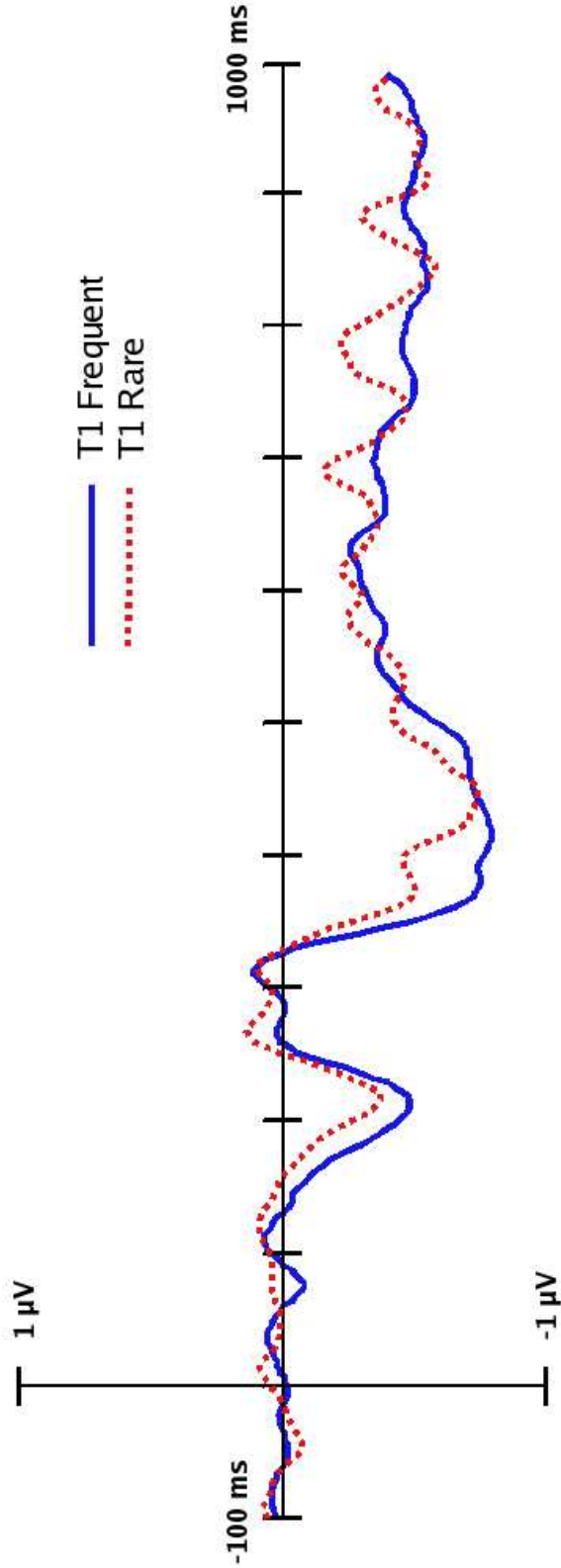


Figure 9

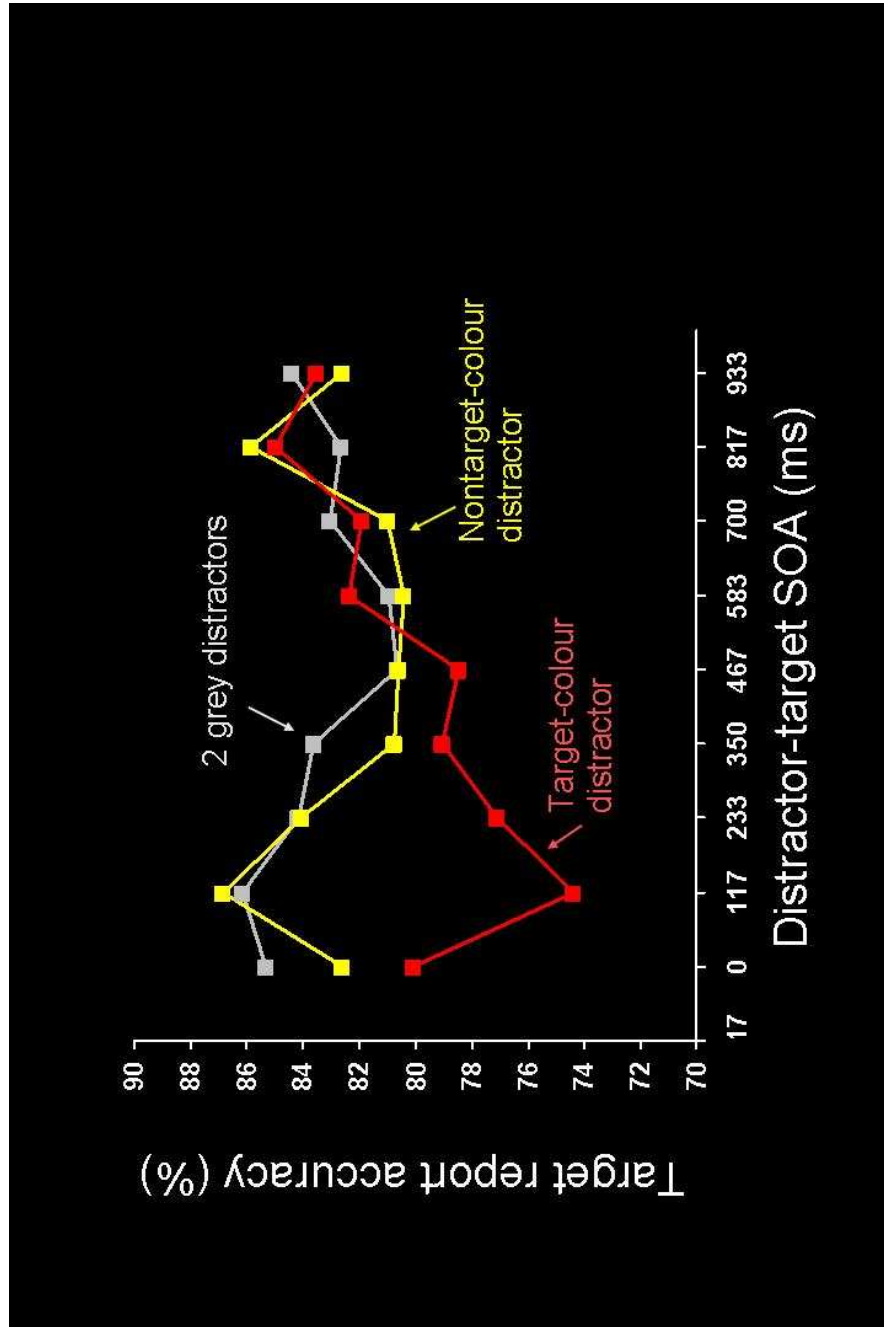


Figure 10

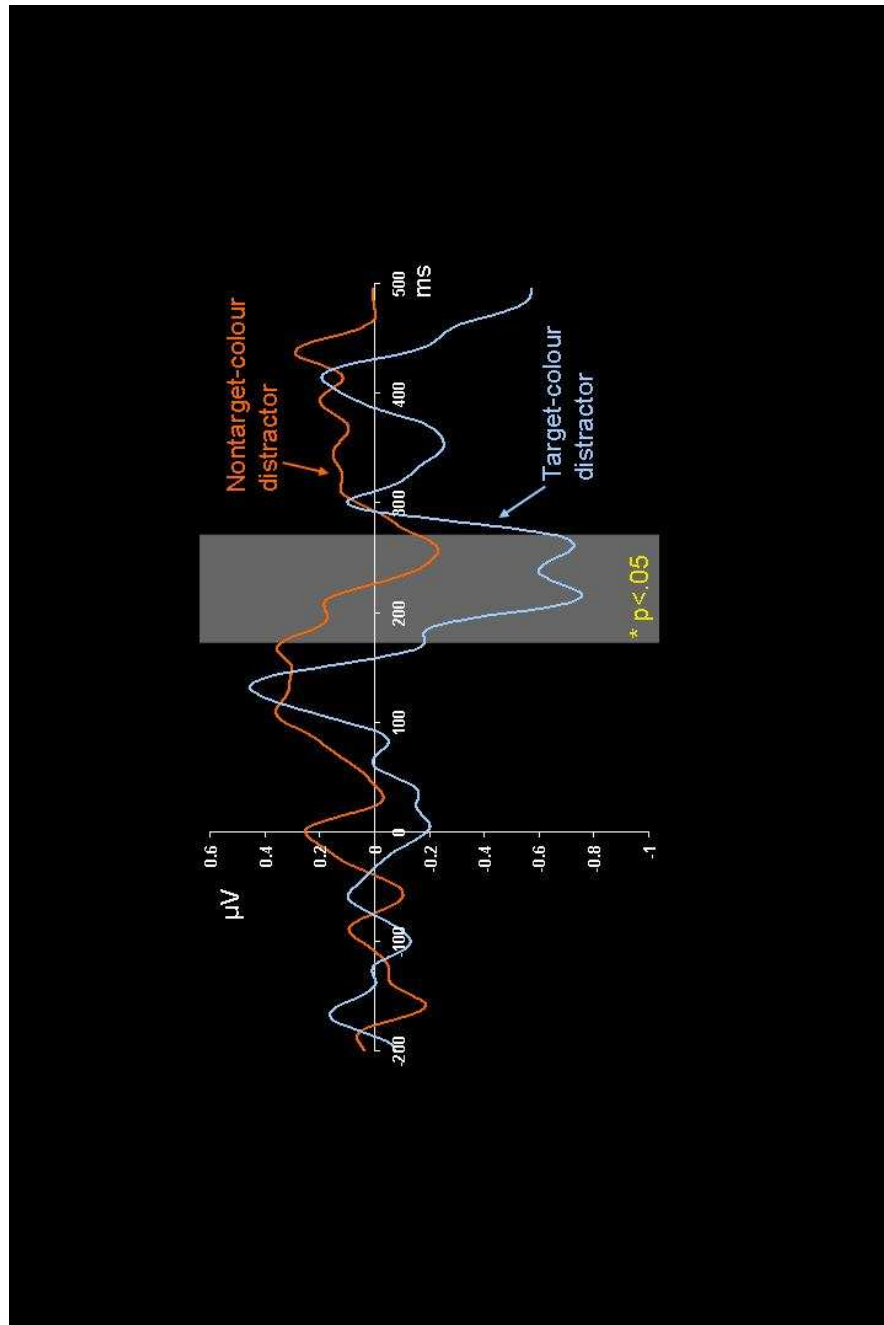


Figure 11

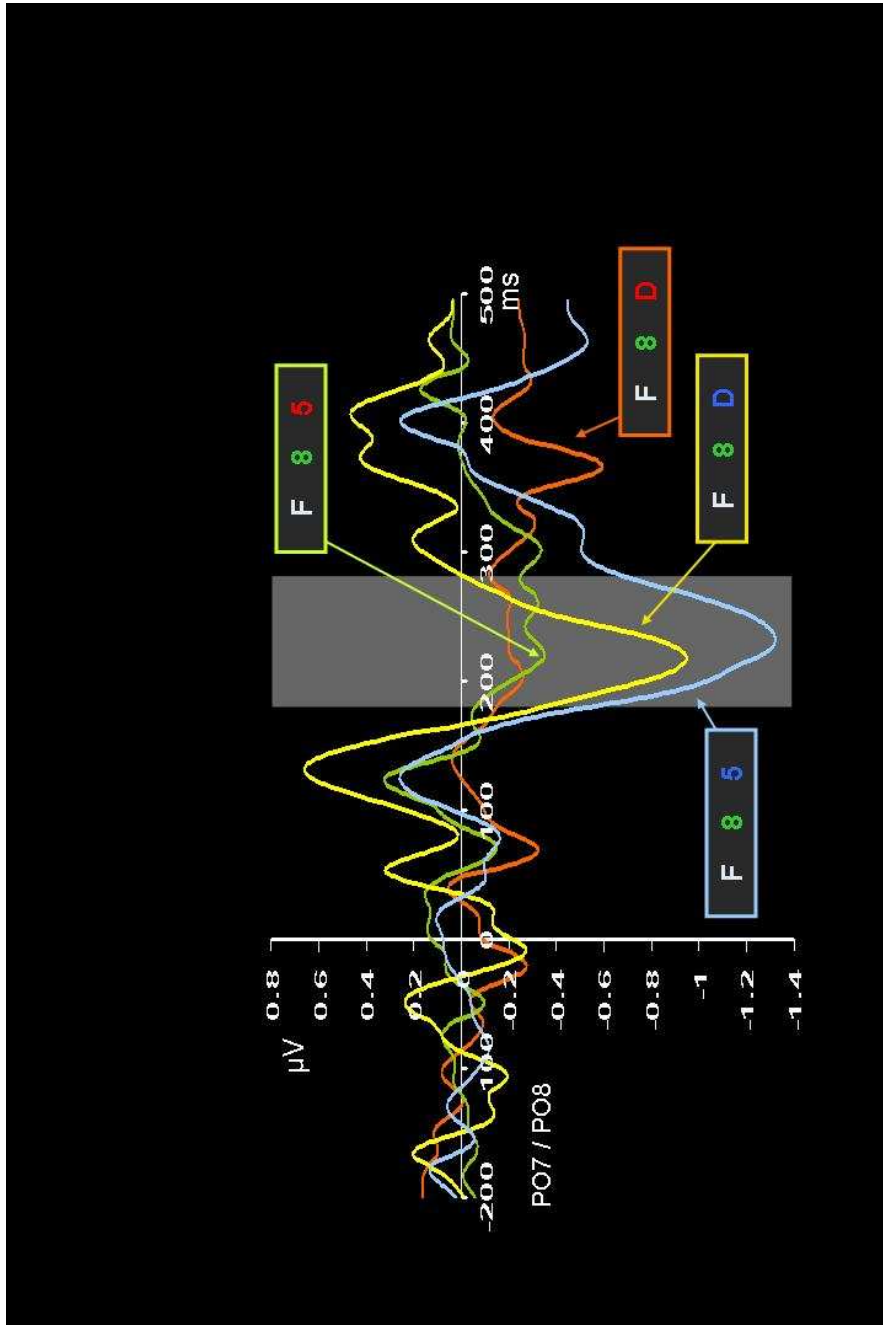


Figure 12

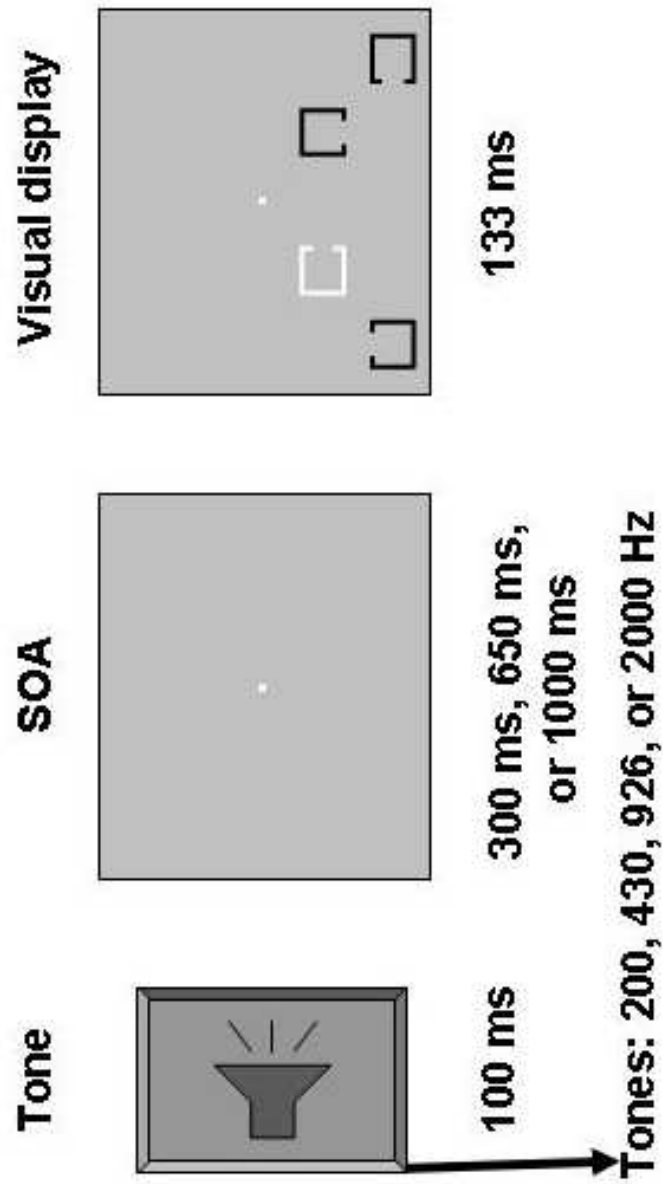


Figure 13

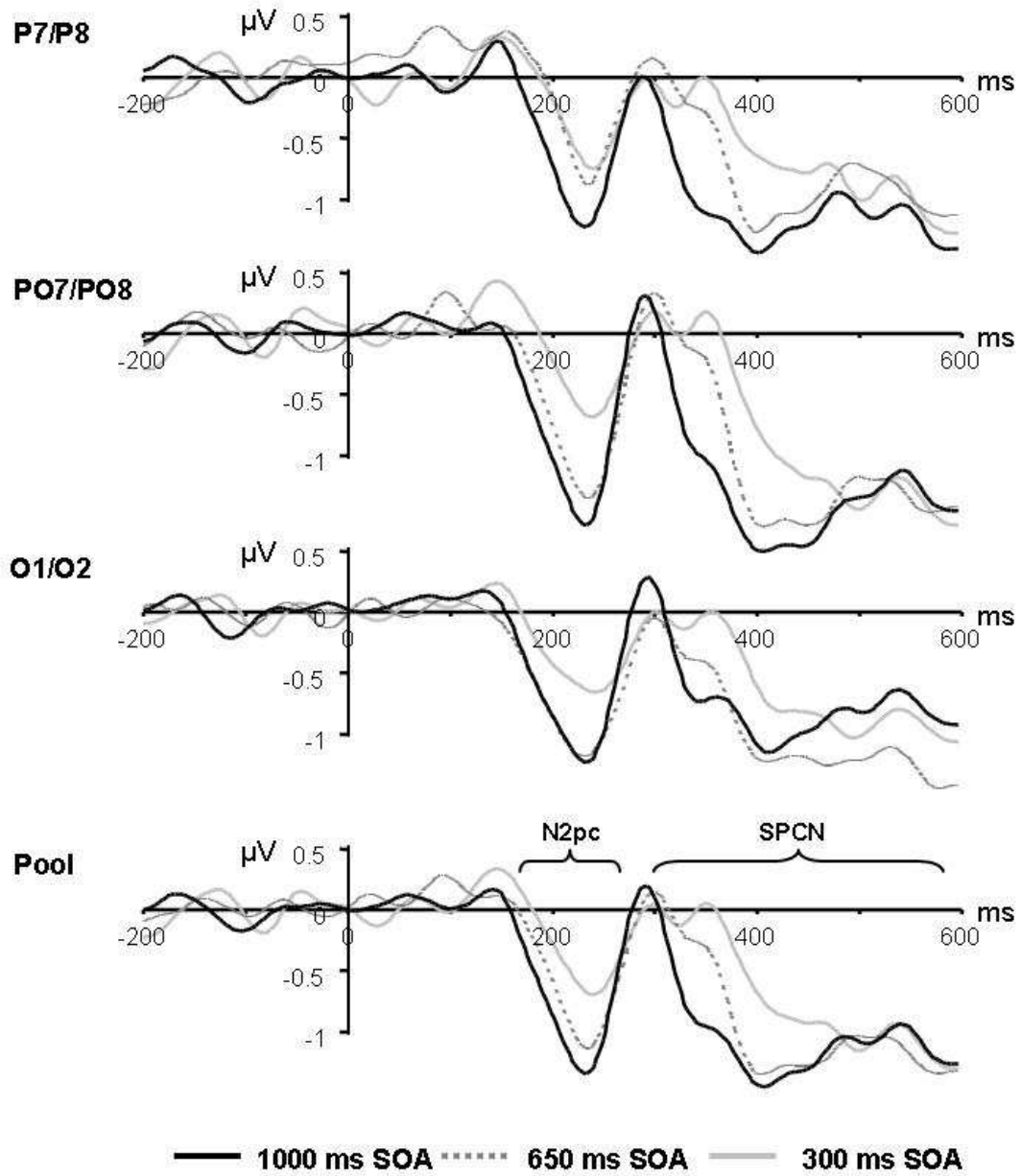


Figure 14

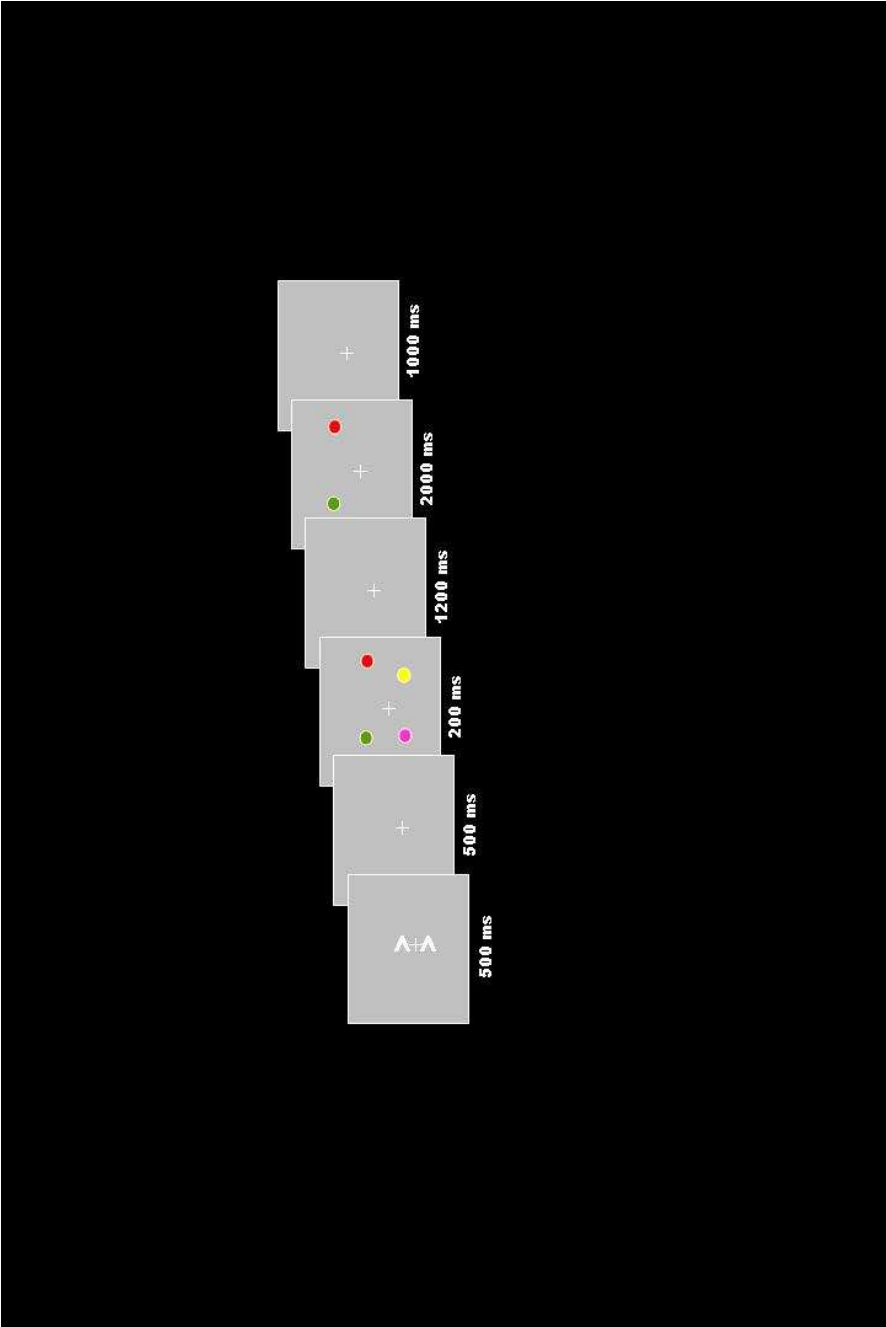


Figure 15

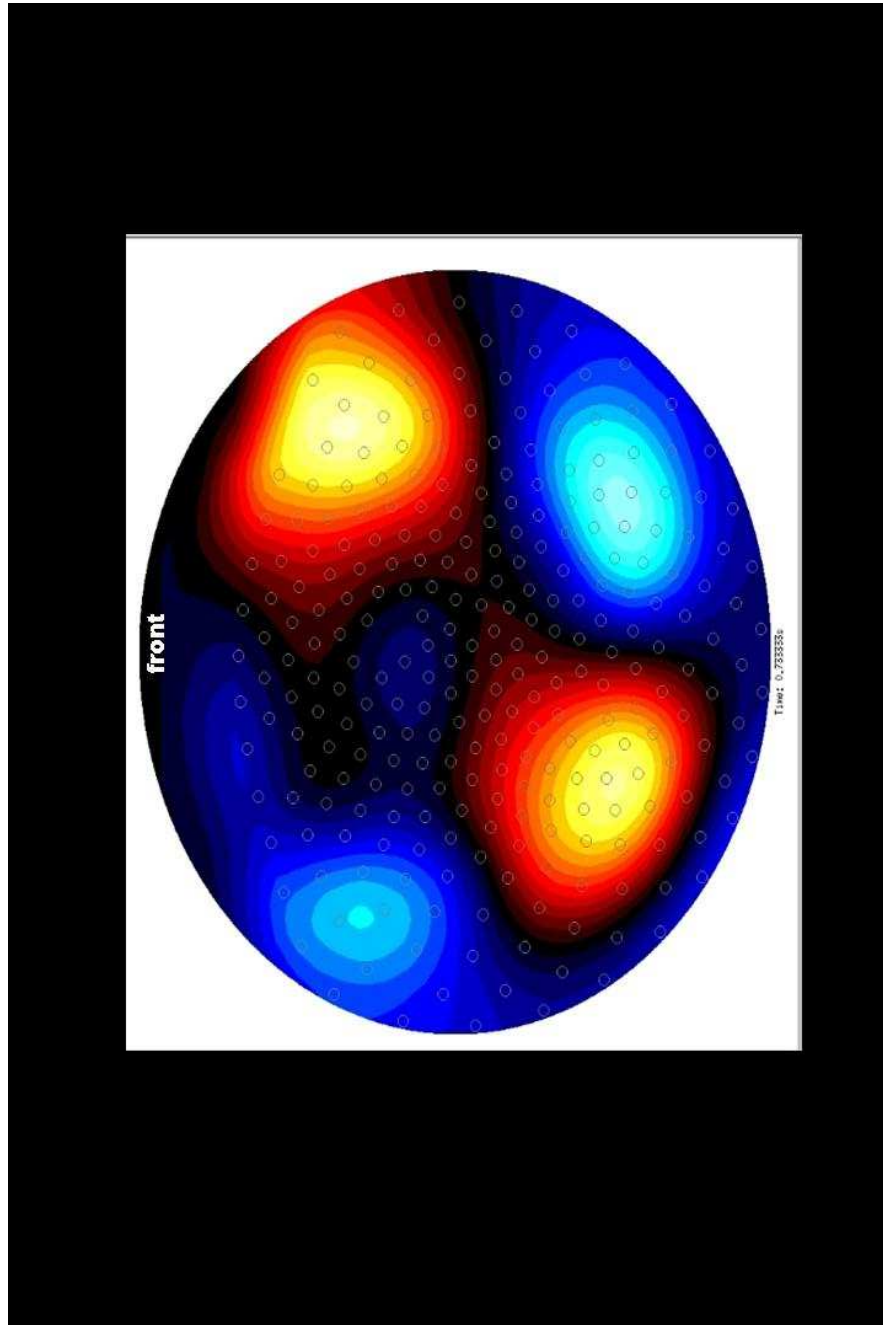
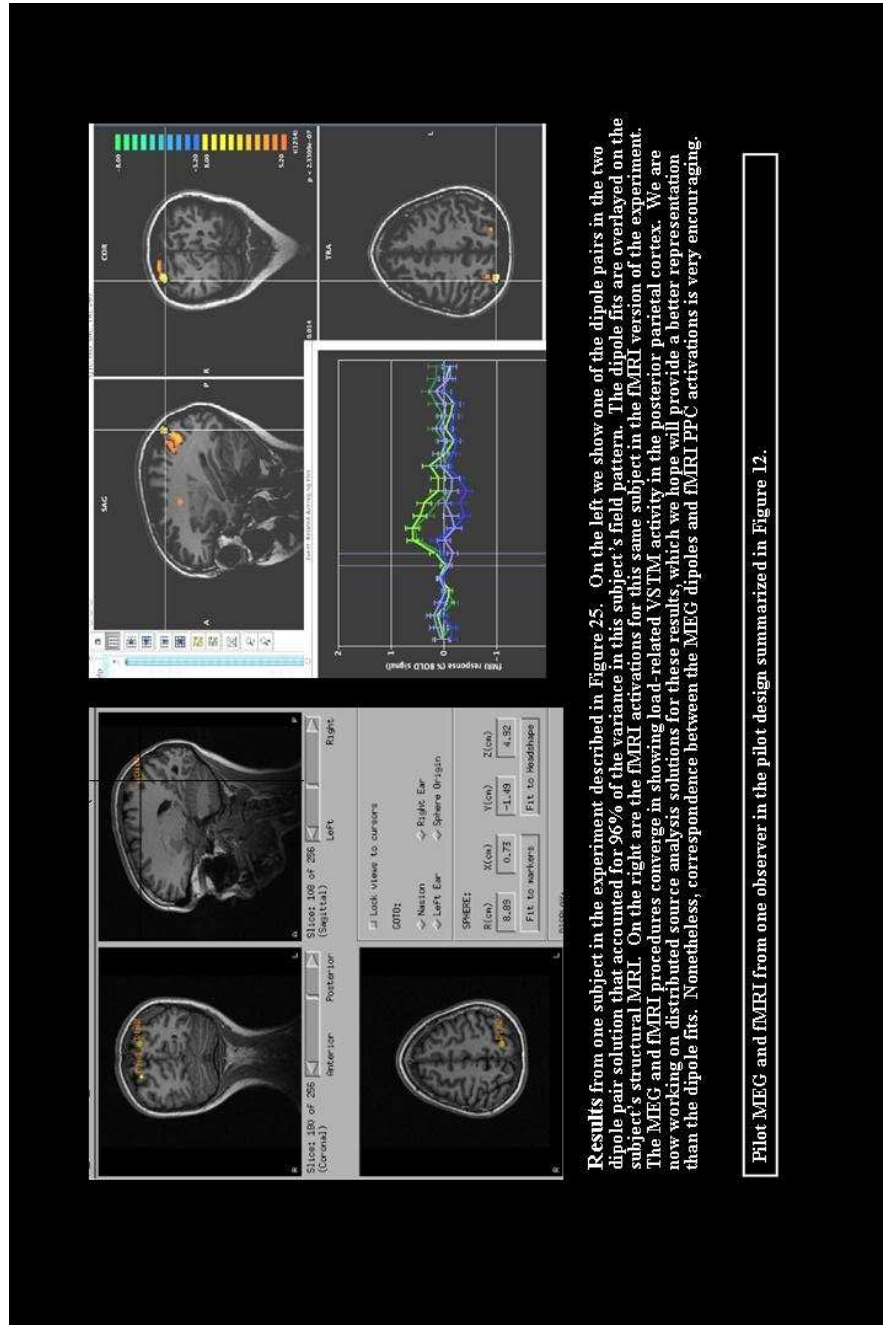


Figure 16



Results from one subject in the experiment described in Figure 25. On the left we show one of the dipole pairs in the two dipole pair solution that accounted for 96% of the variance in this subject's field pattern. The dipole fits are overlaid on the subject's structural MRI. On the right are the fMRI activations for this same subject in the fMRI version of the experiment. The MEG and fMRI procedures converge in showing load-related VSTM activity in the posterior parietal cortex. We are now working on distributed source analysis solutions for these results, which we hope will provide a better representation than the dipole fits. Nonetheless, correspondence between the MEG dipoles and fMRI PPC activations is very encouraging.

Pilot MEG and fMRI from one observer in the pilot design summarized in Figure 12.

Figure 17

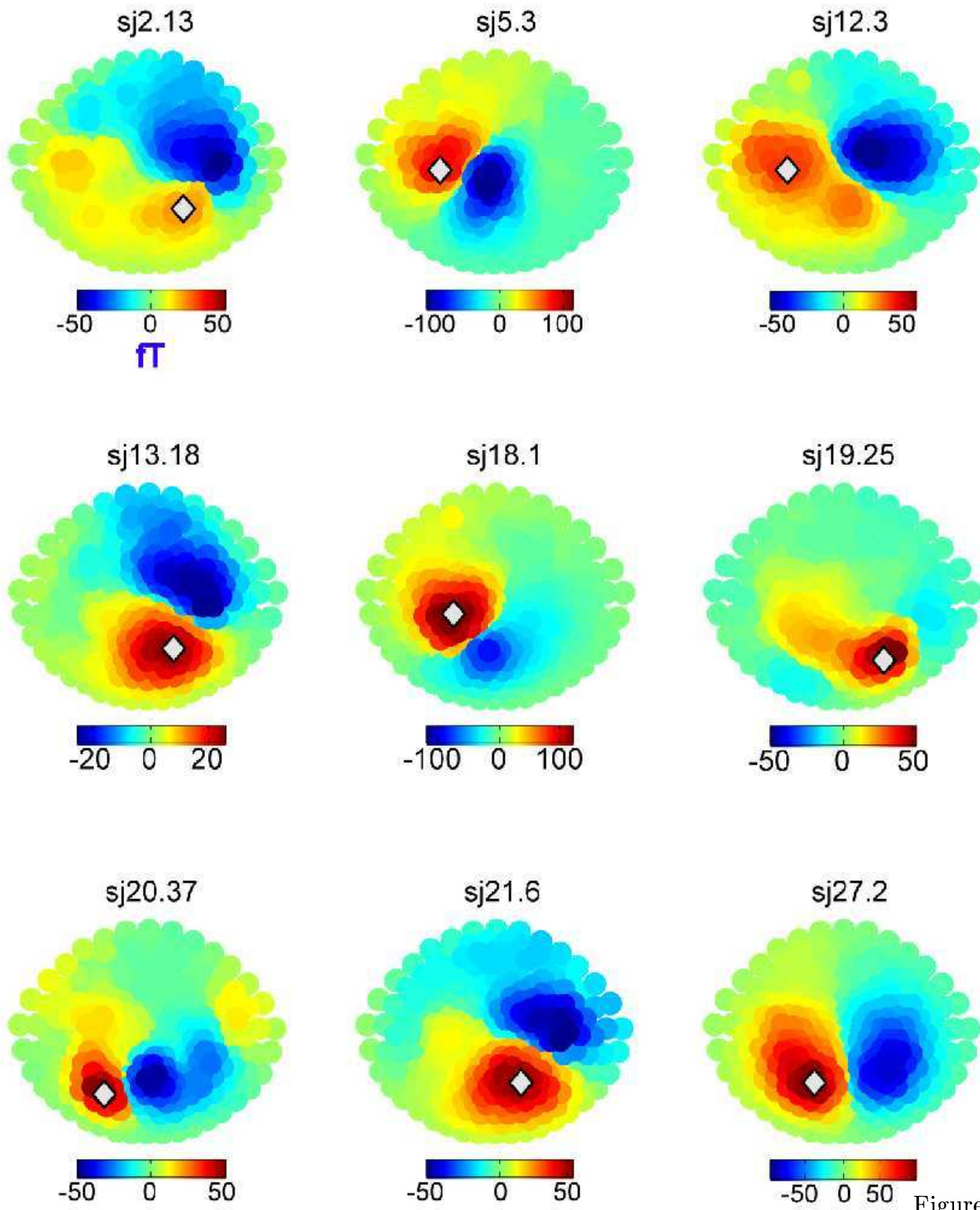


Figure 18

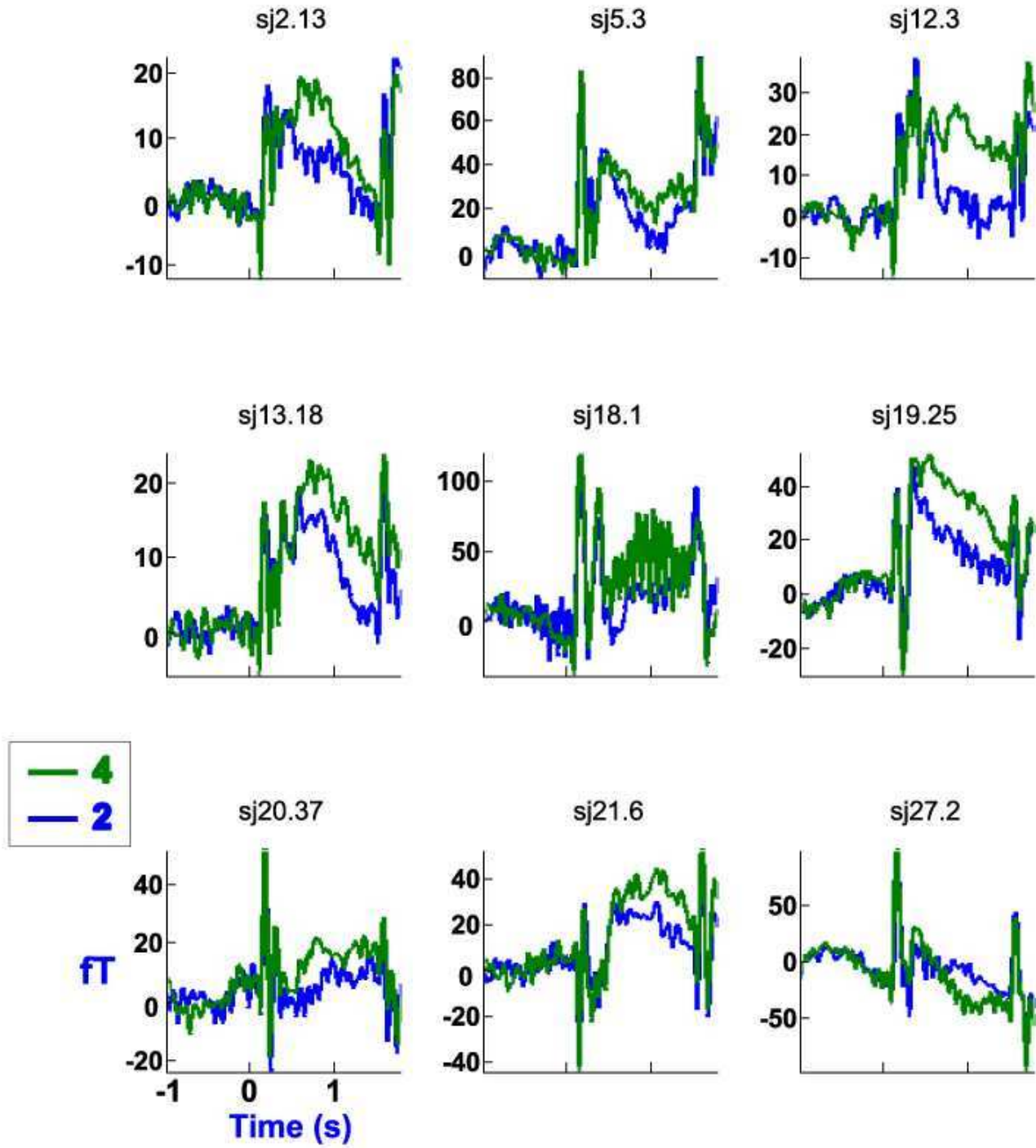


Figure 19

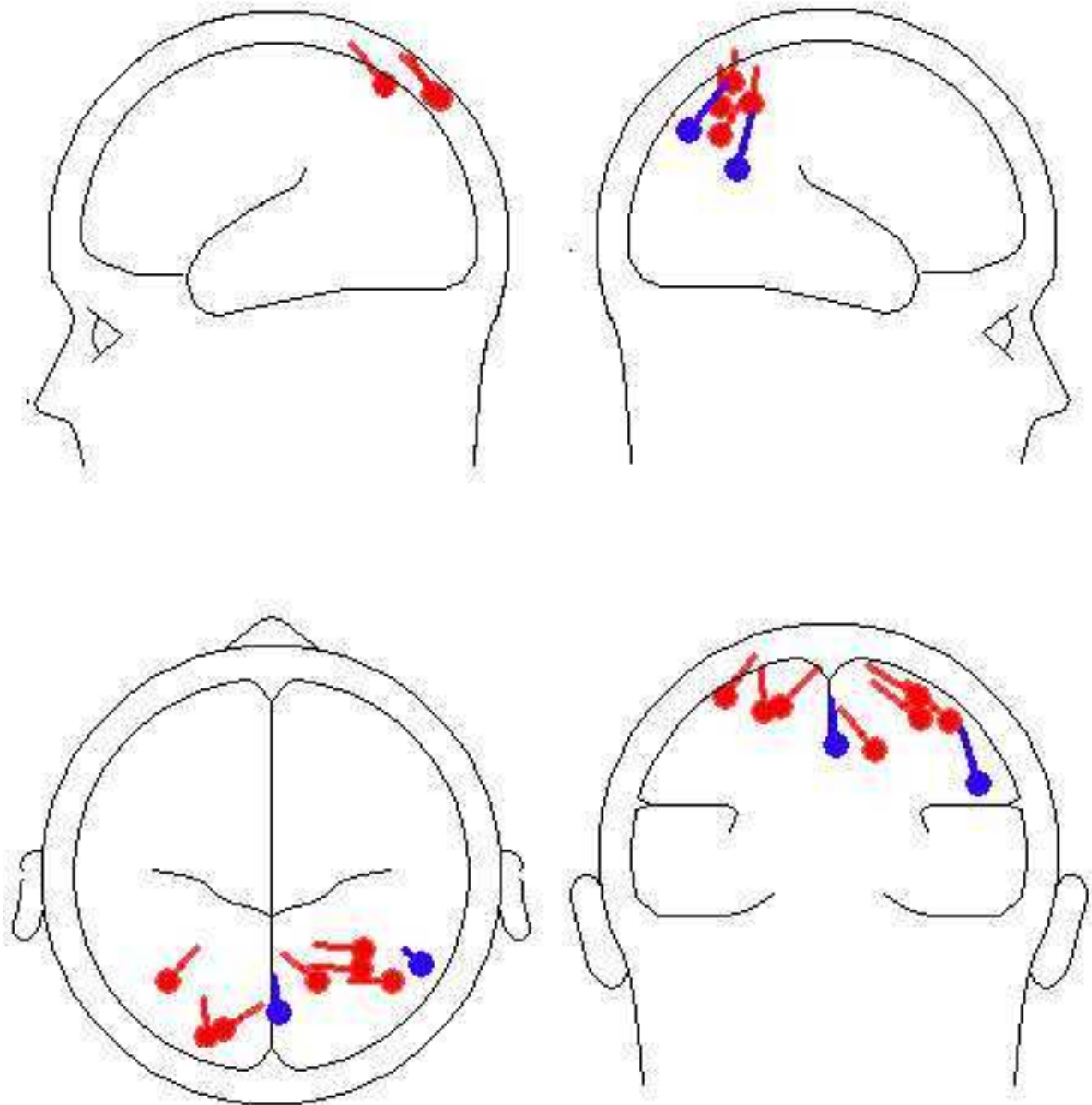


Figure 20

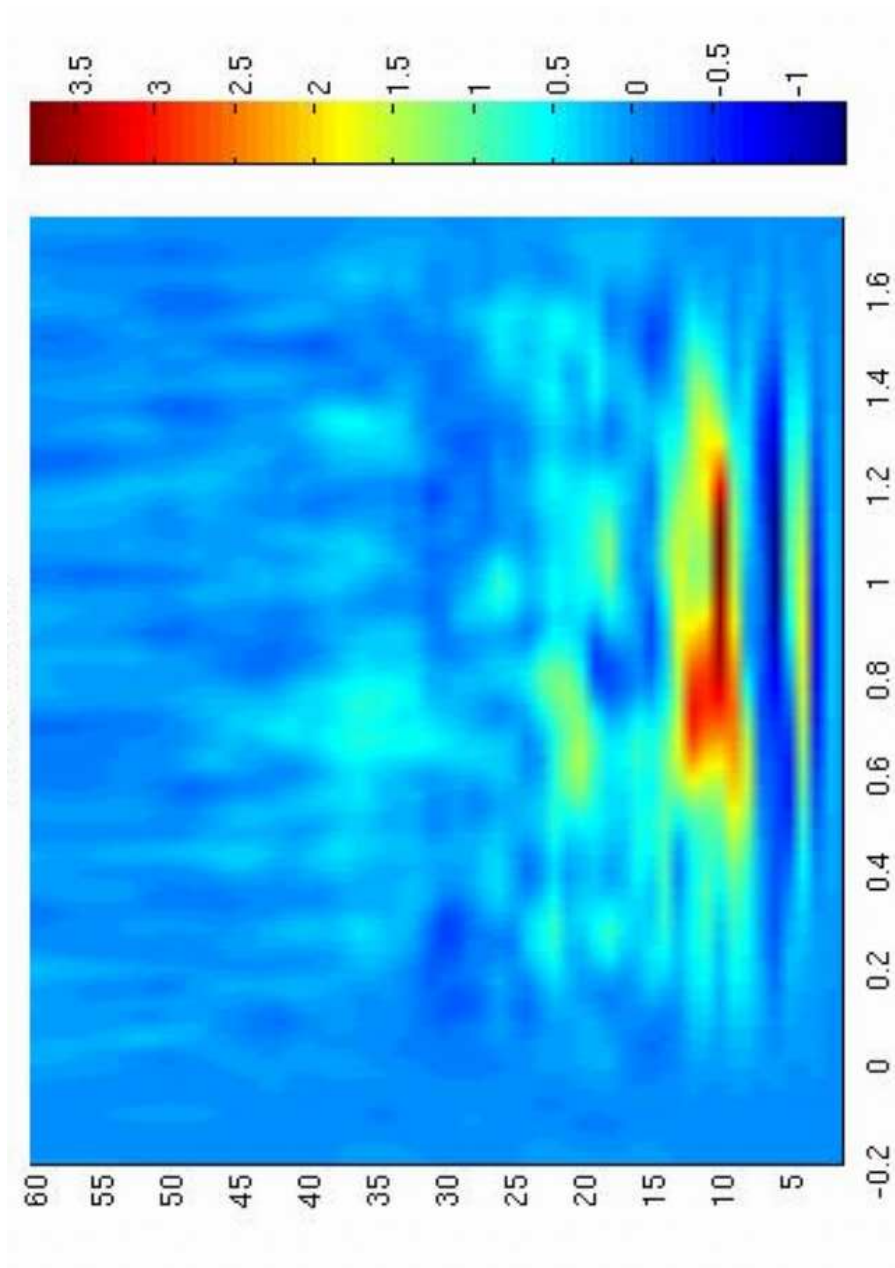


Figure 21

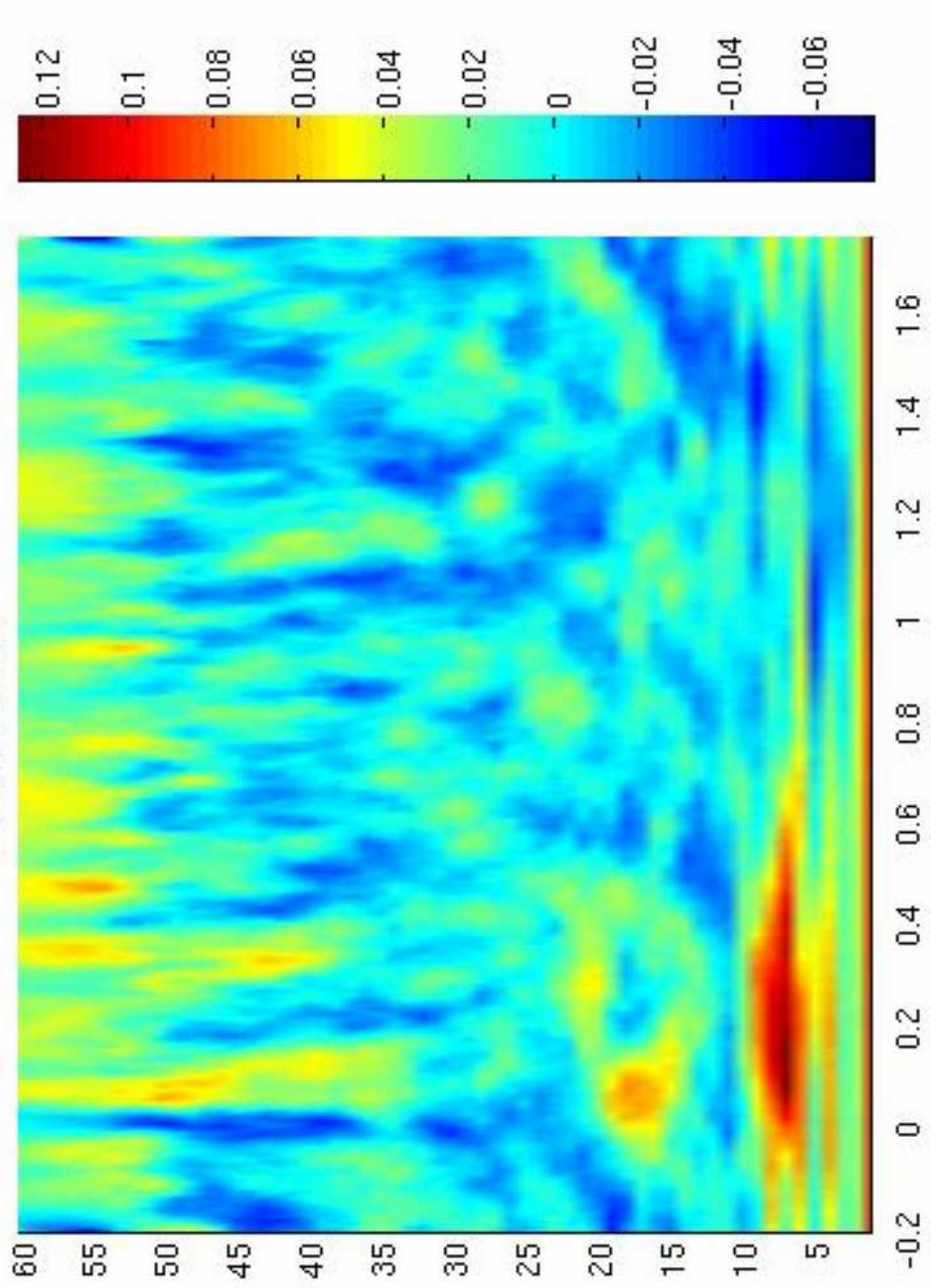


Figure 22

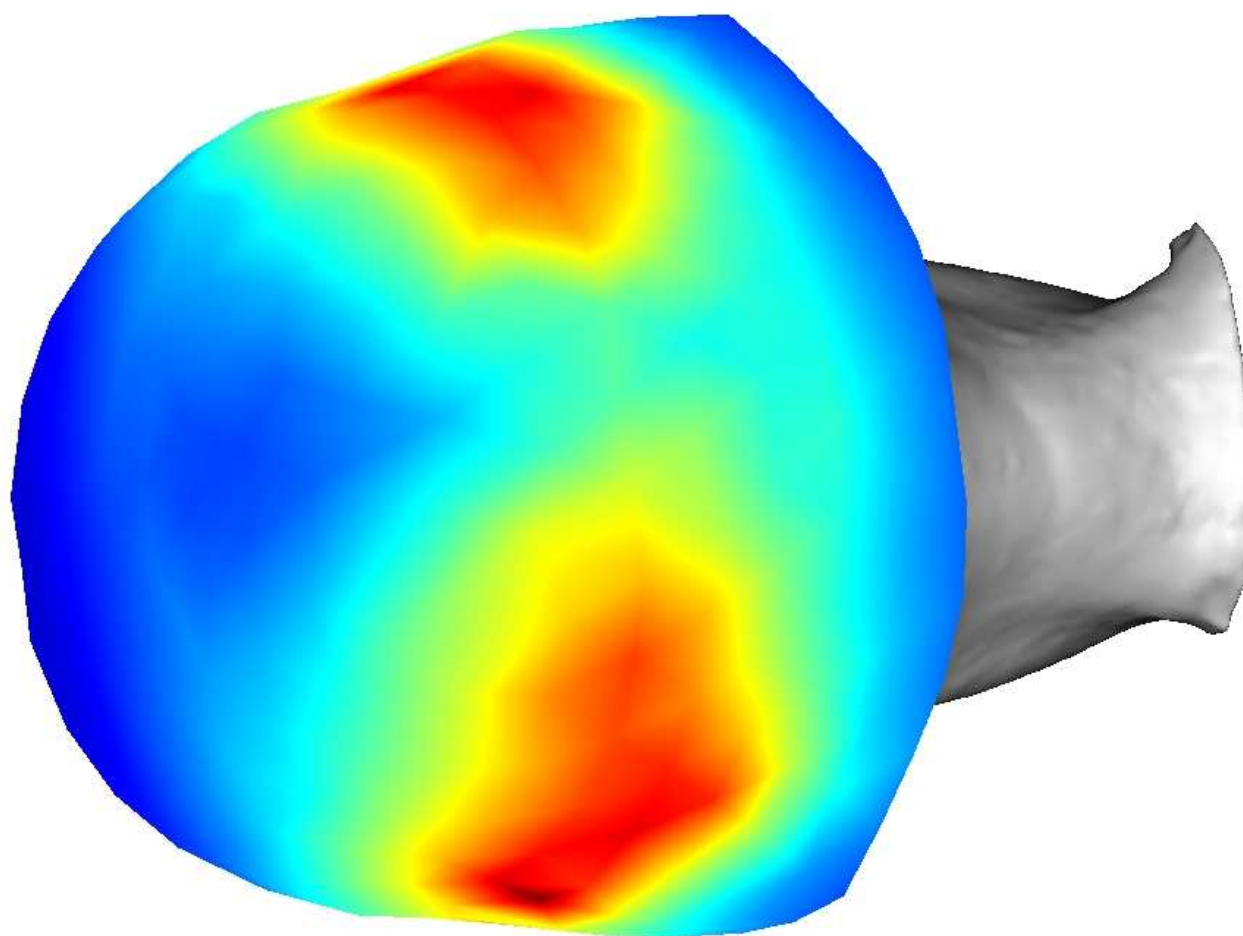


Figure 23

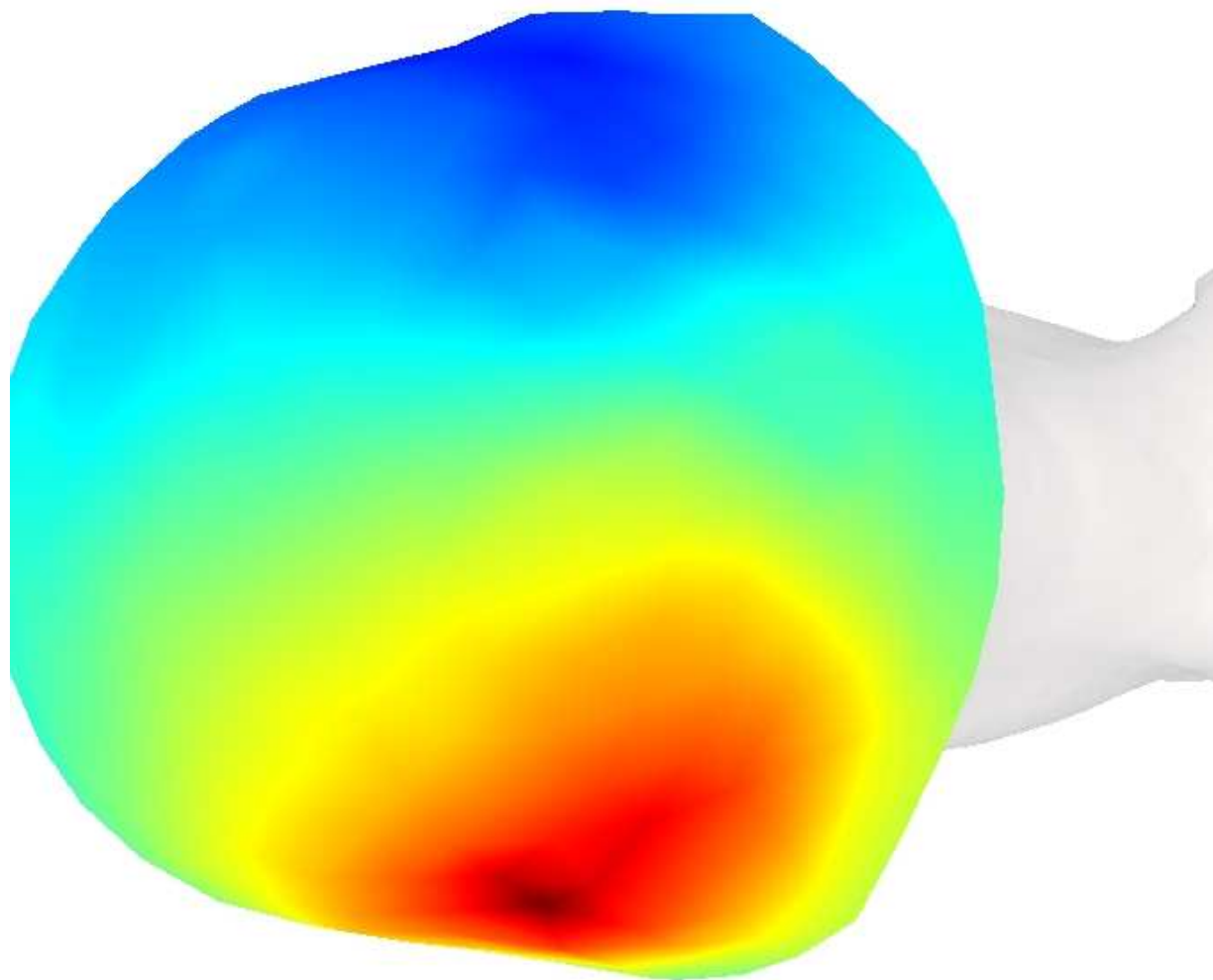


Figure 24

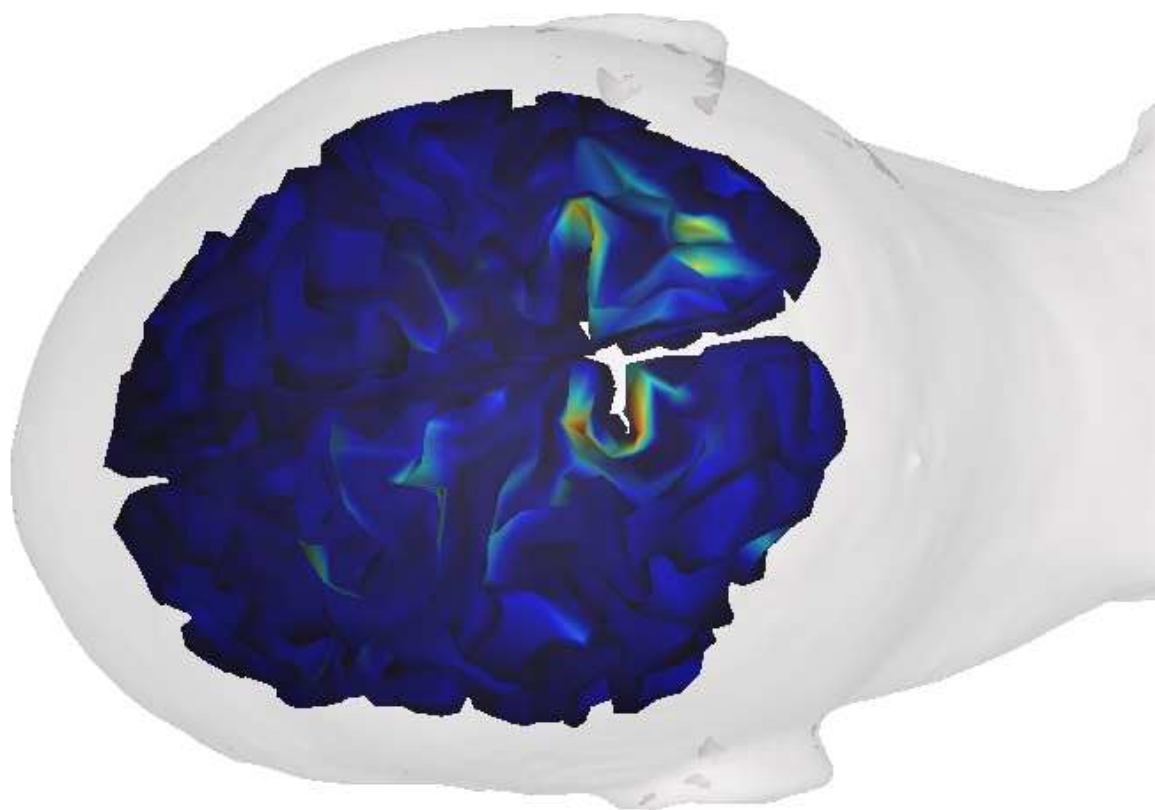


Figure 25