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Electrophysiological evidence of enhanced cortical activity in the human brain during visual curve tracing

Christine Lefebvre [a], Pierre Jolicœur [a,*], Roberto Dell'Acqua [b]

[a] Département de Psychologie, Université de Montréal, C.P. 6128, Succursale Centre-Ville, Montréal, Québec, Canada H3C 3J7
[b] DPSS, Via Venezia 8, 35131 Padova, Italy

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ABSTRACT

ERPs were recorded while participants performed a curve tracing task in which they had to identify the end point of a target curve presented among three other distractor curves. Differential activation associated with the side of the target curve was found in the form of a sustained posterior contralateral negativity (SPCN). This contralateral brain activity suggests covert attention was deployed to the target curve during performance of the tracing task. The amplitude of the SPCN varied according to the hypothesized curve-tracing process, depending on whether the start and end locations of the target curve were above to below the horizontal midline, or the opposite, and this detailed analysis of the results provided evidence supporting the spread-of-attention model of curve tracing. These results represent the first neurophysiological investigation of brain activity reflecting visual curve tracing in humans.

1. Introduction

Curve tracing is the process by which a visual contour is covertly followed over visual space. This process was postulated to be of fundamental importance for processing the spatial structure of visual scenes (Ullman, 1984). It was first studied by Jolicœur, Ullman, and Mackay (1986). They found that the time taken to decide if two landmarks were on the same curve or not was greater when the distance between them, along the curve, was increased. Because this curve-distance effect occurred even though the Euclidian distance between the landmarks was constant, Jolicœur et al. (1986) concluded that participants were internally tracing the curves when they performed the task. Curve tracing is believed to be covert because the curve length effect was observed even when eye movements could not be used to follow the curve because the multi curve-displays had been presented for only 180 ms, which was too short to allow useful eye movements (Jolicœur, Ullman, & Mackay, 1991). This is not to say that tracing complex curves, or curves presented in a cluttered display would not require multiple eye movements. Tracing such curves, however, likely involves a combination of coordinated covert (tracing and path-guided shifts of attention) and overt (eye movements) processes.

Jolicœur et al. (1991) also showed that the speed of curve tracing depends on the properties of the curves and the context in which they are embedded. For example, the speed of tracing was slower for contours with greater curvature; and tracing speed decreased as the distance between the target and adjacent curves was narrowed. These effects provided constraints on the possible mechanisms that could be involved in visual curve tracing. They showed evidence of curve tracing using very simple stimuli, as did Pringle and Egeth (1988), who confirmed the basic properties of curve tracing reported by Jolicœur and his colleagues in a set of clever converging experiments. Jolicœur et al. (1991; McCormick & Jolicœur, 1991) hypothesized that tracing could be explained by a beam-like attentional operator travelling along the contour being traced with the rate of tracing determined, in part, by the spatial extent of the region processed by the operator at any given moment (see also, Jolicœur & Ingleton, 1991; McCormick & Jolicœur, 1992, 1994). Further, this model assumes that once the spotlight has travelled on a point of the curve, the activation eventually dies off. This last point has been the subject of controversy, as Roelfsema and colleagues have argued that attention spreads to the curve as it is traced, until the whole of it is activated (Roelfsema, Lamme, & Spekreijse, 2000).

Curve tracing had been studied through behavioural experiments exclusively until Roelfsema and his colleagues (Roelfsema, Lamme, & Spekreijse, 1998; Roelfsema et al., 2000) brought compelling evidence of the involvement of attention in mental curve tracing in a neurophysiological study. In their experiments, monkeys performed a curve tracing task while the firing rates of cells in the monkeys' primary visual cortex was recorded using electrodes implanted in their brain. Two curves were presented on the screen on each trial, both of which terminated at a salient red disk, and one of which also terminated at the fixation point.

* Corresponding author.
E-mail address: christine.lefebvre@umontreal.ca (P. Jolicœur).

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The monkey's task was to saccade to the red disk that was connected to the fixation point by the continuous curve, after the initial fixation point disappeared. Firing rate recording was carried out before the monkey could saccade to the target curve. Importantly, the curves were arranged such that either the target curve (that is, the one that provided a path from the fixation point to one of the red disks) or the distractor curve (the one that did not connect the fixation point to one of the red disks) passed through the receptive field of the recorded neuron. This preparation enabled Roelfsema and his colleagues to record activity in V1 neurons for curves that the monkey presumably traced covertly versus curves that were not traced. Results showed enhanced firing rates when the cell responded to a curve that was the target curve compared to when it was a distractor curve, even though bottom up stimulation was the same in both conditions. Roelfsema and colleagues (Houtkamp, Spekreijse, & Roelfsema 2003; Roelfsema et al., 1998, 2000; Scholte, Spekreijse, & Roelfsema, 2001) argued that the enhanced firing rate of visual neurons can be considered as the neuronal implementation of the spread of attention on the target curve during curve tracing. Moreover, they also argued that as attention spreads, the whole curve becomes activated. Houtkamp et al. (2003) provided evidence of this whole-object effect by showing that participants were better aware of a change in the beginning of a target curve being traced than a change in a distractor curve, well after they had moved on to trace a later part of the target curve, which could not be the case if activation had died off as tracing continued and the attentional spotlight was operating elsewhere, as the spotlight model predicts. However, Crundall, Dewhurst, & Underwood, 2008, argued that the task itself (asking participants if they had noticed the change) biased participants into doing the task differently, and allocate resources to previously traced sections of the curve which they would no longer have attended to otherwise (but see Roelfsema, Houtkamp & Korjoukov, in press, for a reply). This question, of whether a spotlight moves on a contour or spreads on it, is central to the understanding of how attention works, and this paper aims at providing new evidence to help settle the debate.

The first goal of the present study was to provide, for the first time, evidence of differential brain activity caused by visual curve tracing in the human brain. To do so we recorded electrical activity of the brain using electroencephalography while participants performed a curve tracing task, and we analyzed the signals using the event-related potentials (ERPs) method (Luck, 2005).

We used an ERP component related to the processing of visual stimuli that is also sensitive to target location, namely the *S*ustained *P*osterior *C*ontralateral *N*egativity (SPCN; see Jolicœur, Brisson, & Robitaille, 2008; Jolicœur, Sessa, Dell'Acqua, & Robitaille, 2006). When relevant stimuli presented laterally are attended, a sustained, increased negativity is observed at posterior sites contralateral to the target, compared to activity measured at corresponding ipsilateral sites. This lateralized potential is measured in the presence of visually equivalent, but irrelevant stimuli presented on the side opposite to the target, in order to equate low-level, bottom-up, sensory activation. The SPCN component is believed to reflect encoding and active maintenance of visual stimuli in short-term memory (VSTM, Jolicœur et al., 2008; Perron et al., 2009). However, Drew and Vogel (2008), as well as Klaver, Talsma, Wijers, Heinze, and Mulder (1999), provided evidence that such a component is not only an index of retention of items in VSTM, but is also observed during processing of ongoing stimulation. In their task, Drew and Vogel (2008) identified an SPCN while participants tracked multiple objects moving in the left of right hemifield. Similarly, Klaver and colleagues (1999) observed an SPCN during presentation of to-be-memorised items, as well as during the stimulus-free retention interval. In light of these results, we expected to observe an SPCN during the processing of laterally-presented curves in a curve tracing task.

Our hypothesis, therefore, was that if curve tracing is performed by a local attentional enhancement of the target curve, and this curve is presented either in the left or right visual field, this should produce differential lateralization of electrical activity in visual cortex. We expected this would be observed as an increased negativity at posterior electrode sites contralateral to the target curve, compared with activity recorded at corresponding ipsilateral sites. Because curve tracing is a process that is extended in time, and that there is psychophysical and single-unit electrophysiological evidence for sustained responses to attended curves in the visual cortex of monkeys, we expected to observe a sustained response in our ERPs. In other words, we expected to observe a significant SPCN waveform with the side of the effect determined by the location of the target curve in the visual display. To test this hypothesis, we designed a task in which participants had to determine the colour of a disk positioned at the end of one of four curves presented simultaneously in the visual field, as illustrated in Fig. 1. Two of the curves, in every trial, were in the left visual field, and two were in the right visual field. The target curve was cued by the prior presentation of an empty white disk at the end of that curve (Fig. 1). Although all of the curves were in either left or right visual fields, their endpoints were on the vertical midline. This procedure had two advantages. First, the starting and end points of the curves were not lateralised, and so processing of stimuli at these locations could not produce an SPCN. In fact, only processing of the lateralised portion of the curve could produce an SPCN, therefore eliminating possible confounds brought by processing that is not specifically related to visual curve tracing (in particular, target cue starting point detection and target end point identification).

The second goal of this paper was to provide evidence about how attention is deployed on a curve, that is, if attention moves on the curve in the manner of a spotlight, or if it spreads over the curve, eventually activating a representation of the entire curve. To do so, we used a characteristic of the SPCN, namely that

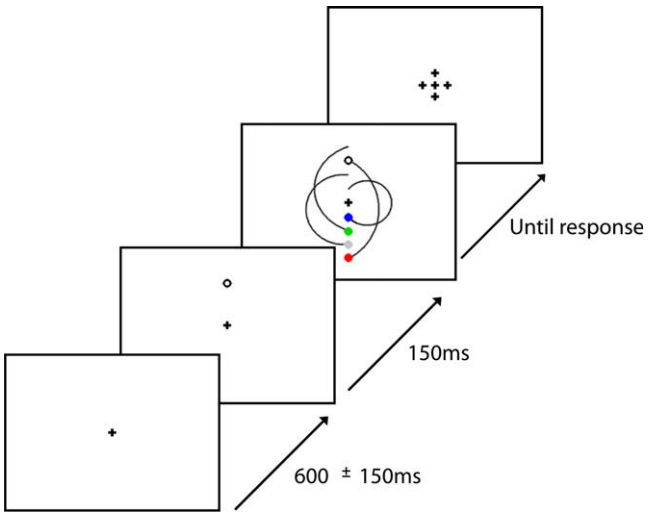

Fig. 1. Illustration of the stimuli and trial sequence. A fixation cross appeared at the centre of the screen when participants initiated a trial. It was followed by the addition of the target cue, an empty white circle, 500 ms (±150 ms) later. The cue and fixation were completed by the remainder of display 150 ms later. This test display consisted of 4 curves, of equal length and thickness. The display remained on the screen until 500 ms after a response was entered. It was then replaced by a feedback cross made of minuses or pluses, depending on accuracy on the previous trial. The background and target curve colours were inverted in the figure for clarity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

stimuli presented in the lower hemifield tend to yield a larger SPCN than stimuli presented in the upper hemifield (Perron et al., 2009). In the task we used, target curve starting points were either in the upper or lower hemifield (see Fig. 1) and the endpoints were in the opposite hemifield. If SPCN amplitude is larger for stimuli in the lower hemifield, then it should also be larger when a curve is traced below fixation than when tracing occurs above fixation. This means that in our task, SPCN amplitude should change during the course of tracing. The way amplitude should change is different depending on if attention 'spreads' to the whole curve or moves along it. In both cases, lower hemifield-starting target curves should yield a larger initial amplitude than upper-hemifield-starting curves. Once the lower hemifield-starting curve crosses over to the upper hemifield, then the spotlight model predicts SPCN amplitude should decrease, whereas the attention-spread model predicts it should remain stable, as the 'lower' part remains activated. In the case of upper-starting targets, both models make the same prediction: SPCN amplitude should be larger once the lower part is being traced, than at the beginning when the upper part is being traced.

2. Methods

2.1. Participants

Forty students from Université de Montréal participated in this experiment. Twelve of them were male (and thus 28 were female), and one was left handed. Their mean age was 22 years (SD = 2.78). All reported normal or corrected-to-normal vision and no history of neurological disorder. They received a monetary compensation of 20$CAN and gave informed consent prior to their participation. Data from five participants were rejected from analysis (see below).

2.2. Apparatus

Participants were seated 57 cm from a computer screen (17″ CRT colour monitor, 640 × 480 pixels at 60 Hz) in a dimly lit, electrically shielded room. Their head position was secured by a chin rest. Stimulus presentation and behavioural data recording was controlled via E-Prime® software. Participants entered their responses using four adjacent keys on a standard computer keyboard.

2.3. Stimuli

Stimuli consisted of white curves (CIE $x = .277$, $y = .307$, $Y = 36$ cd/m^2), identical in length and width, displayed on a black (CIE $x = .403$, $y = .445$, $Y = .14$ cd/m^2) background (see Fig. 1). One of the curves, the target curve, had an empty white circle as a starting point, whereas the other curves had none. The end points of the curves was either a red (CIE $x = .612$, $y = .343$, $Y = 13.6$ cd/m^2), green (CIE $x = .298$, $y = .578$, $Y = 20.2$ cd/m^2), blue (CIE $x = .151$, $y = .075$, $Y = 7.65$ cd/m^2), or white (CIE $x = .277$, $y = .307$, $Y = 36$ cd/m^2) disk. The four curves started at one of four positions above or below fixation, namely 0.75°, 1.5°, 2.15°, and 2.9°, and ended in one of the same positions in the opposite hemifield (see Fig. 1). Two curves were located to the right of fixation and two curves, to the left. The curves extended to at least 0.75° and at most 2.4° from the vertical midline to the point of maximum distance. Thus, on average, the curves produced the same amount of bottom-up sensory activation in the left and right cerebral hemispheres.

2.4. Procedure

Each participant completed one session of testing including 32 practice trials and 480 experimental trials. The target curve was presented to the left of fixation on half of the trials and to the right of fixation on the other half. In half of left-target curve trials and in half of the right-target curve trials, the curves started above fixation and finished below fixation, whereas the reverse occurred in the other half of left- and right-target curve trials.

Trials started with a feedback cross made of a set of plus or minus signs, depending on the response accuracy on the preceding trial. The first trial in a block started with a plus sign cross. Participants initiated a trial by pressing the space bar when ready. The feedback was immediately replaced by a small fixation cross at the centre of the screen. Participants were told to maintain fixation on this cross, which remained on the screen until 500 ms after they made their response. It remained alone on the screen for an average of 600 (±150 ms jitter). An empty white circle, cueing the starting point of the target curve, then appeared on the screen. One hundred and fifty ms later, the four curves terminated by coloured disks followed. In the opposite hemifield (upper or lower) of the cue circle, curves ended with a coloured disk positioned on the vertical midline (Fig. 1). This display remained on the screen until the participant entered a response or until 3000 ms after its appearance on the screen. The task was to determine the colour of the disk at the end of the target curve cued by the empty white circle. Half the participants used their right hand to press the 'b' (white), 'n' (blue), 'm' (red), or ',' (green) keys on the keyboard, whereas the other half used their left hand to press the 'z' (white), 'x' (blue), 'c' (red), or 'v' (green). Participants were instructed to respond as accurately as possible, and as fast as possible.

2.5. Electrophysiological recordings

Brain electrical activity was recorded continuously, at a sampling rate of 256 Hz (low-pass filtered at 67 Hz), using a BioSemi Active Two system and an elastic head cap with 64 Ag/AgCl active electrodes at standard 10–10 system positions. In addition, signals from six external electrodes were recorded. Electrodes were applied to the left (HEOGl) and right (HEOGr) outer canthi, and above (VEOGu) and below (VEOGd) the left eye. An electrode was also applied to each mastoid. HEOG and VEOG waveforms were obtained by subtracting left HEOG from right HEOG and VEOG up form VEOG down, respectively. The signal was re-referenced offline to the average mastoids.

Each channel was filtered with a 0.1 Hz, 12 dB/octave high-pass filter. Trials with HEOG or VEOG activity varying by more than 50 μV over a 100 ms period were removed from analyses, as were trials with EEG activity varying by more than 100 μV over a 50 ms period at electrodes PO7/O8. For all other electrodes, signal was removed for the flagged electrode only, if voltage varied by more than 100 μV in a 50 ms period. Incorrect trials were also removed from analysis. If, after artefact and error removal, less than 50% of the trials for one participant were left, data from that participant was removed from analysis. This was the case for five of the participants: one participant was removed because of chance performance, and four others were removed because of excessive rate of ocular movements.

For each participant, we also averaged the HEOG separately for left-target curve trials and for right-target curve trials. This average HEOG reached a maximum of 3 μV, implying that eye movements were in the order of less than .1° towards the target curve. The resulting waveform, averaged over 35 participants, is shown at the bottom of Fig. 2.

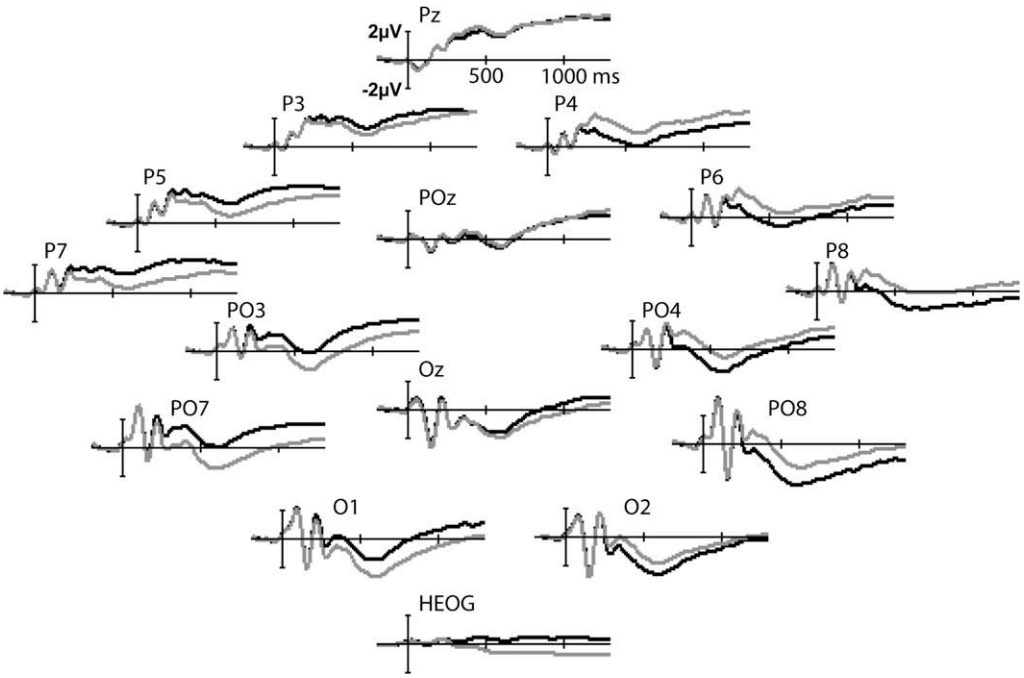

Fig. 2. Grand average waveforms (μV) at electrodes Pz, P3, P4, P5, P6, P7, P8, POz, PO3, PO4, PO7, PO8, Oz, O1, O2, and HEOG, for trials with the target curve in the left visual field (black lines) or the target curve in the right visual field (grey lines), from 200 ms before the apparition of the curves until 1300 ms after. The waveforms were filtered with a 10 Hz, 48 dB/octave low-pass filter for display purposes only.

3. Results

3.1. Behavioral data

Mean accuracy was 92%. We averaged accuracy for each of the 35 participants separately for left and right trials, and trials starting below and above fixation, and compared them in an ANOVA with side (left vs. right) and hemifield (lower vs. upper) as within-subjects factors. No main effect nor interaction was found, all *p*s > .10. Response times (RTs) were analyzed in the same manner. This time, a main effect of side was found: target curves on the left side (mean: 1568 ms) were traced faster than targets on the right side of fixation (mean: 1608 ms), $F(1, 34) = 8.51$, $MSE = 6792.67$, $p < .007$. Target side did not interact with target starting point ($p > .95$), and there was no main effect of starting point either ($p > .82$).

3.2. Electrophysiological data

Fig. 2 shows waveforms for left (black lines) and right (grey lines) stimuli for parieto-occipital electrodes P7, P5, P3, PO7, PO3, O1, Pz, POz, P4, P6, P8, PO4, PO8, and O2. As is evident from the figure, lateral electrodes show a reversed relation between left and right stimulation. Left-side electrodes show more negative values for stimuli presented on the right than on the left of fixation. Conversely, electrodes positioned on the right side of the head show more negative values for stimuli presented on the left side than on the right side of fixation. Amplitude values are slightly more negative, overall, on the right side of the head than on the left side; however, the difference between ipsi and contralateral waveforms was the same on both sides of the scalp.

To calculate the SPCN, we computed a mean contralateral waveform by averaging the waveform at PO7 for right-target curve trials with the waveform at PO8 for left-target curve trials. We also computed a mean ipsilateral waveform by averaging the waveform at PO7 for left-target curve trials with the waveform at PO8 for right-target curve trials. Finally, we subtracted the mean ipsilateral waveform from the mean contralateral waveform, producing a mean SPCN difference wave. The same calculation was also applied to electrode pairs PO3/PO4, P3/P4, P5/P6, P7/P8, and O1/O2.

The top part of Fig. 3 shows SPCN waveforms for the posterior electrodes mentioned above. An SPCN is clearly visible: the waveforms start to deviate from 0 at about 170 ms after stimulus onset, reach a maximum amplitude of about −1.5 μV at around 300 ms, and show a sustained response for at least 1300 ms after stimulus onset. The maximum SPCN amplitude was near electrodes PO7 and PO8, but neighbouring sites show similar activations, as is typical for the SPCN (Jolicœur et al., 2008). We computed the mean amplitude of the SPCN waveforms at PO7/PO8 for each participant in a window of 300–800 ms, and then submitted these values to a *t*-test against 0. The results confirmed the presence of a significant sustained contralateral negativity associated with curve tracing, $t(34) = -8.79$, $p < .001$). The bottom part of Fig. 3 shows the scalp distribution of the average SPCN during the 300–800 ms interval of our analysis window.

In Fig. 4, we show separate SPCN waveforms for above- and below-fixation starting point trials. In the above-fixation starting point trials (grey line), the SPCN remained stable for the whole length of the time window. In the below-fixation trials, however, the SPCN was larger in amplitude than the above-fixation starting trials at first, but this amplitude difference eventually disappeared. This was verified in an ANOVA comparing the direction of tracing (from above-to-below-fixation and from below-to-above-fixation) at two time windows (data averaged from 400 to 500 ms, or from 1200 to 1300 ms), for the averaged voltage at the 3 sites where the SPCN was largest, namely PO7/PO8, PO3/PO4, and P7/P8 (see top part of Fig. 3). The interaction between direction of tracing and time window was significant, $F(1, 34) = 4.87$, $MSE = 0.49$, $p < .035$. Decomposition of this interaction showed that SPCN amplitude in above-to-below-fixation trials was smaller (−1.00 μV) than below-to-above-fixation trials (−1.43 μV) in the 400–500 ms time window ($F(1, 34) = 14.29$, $MSE = .60$, $p < .002$), but that above- and below-fixation trials amplitude did not differ significantly in

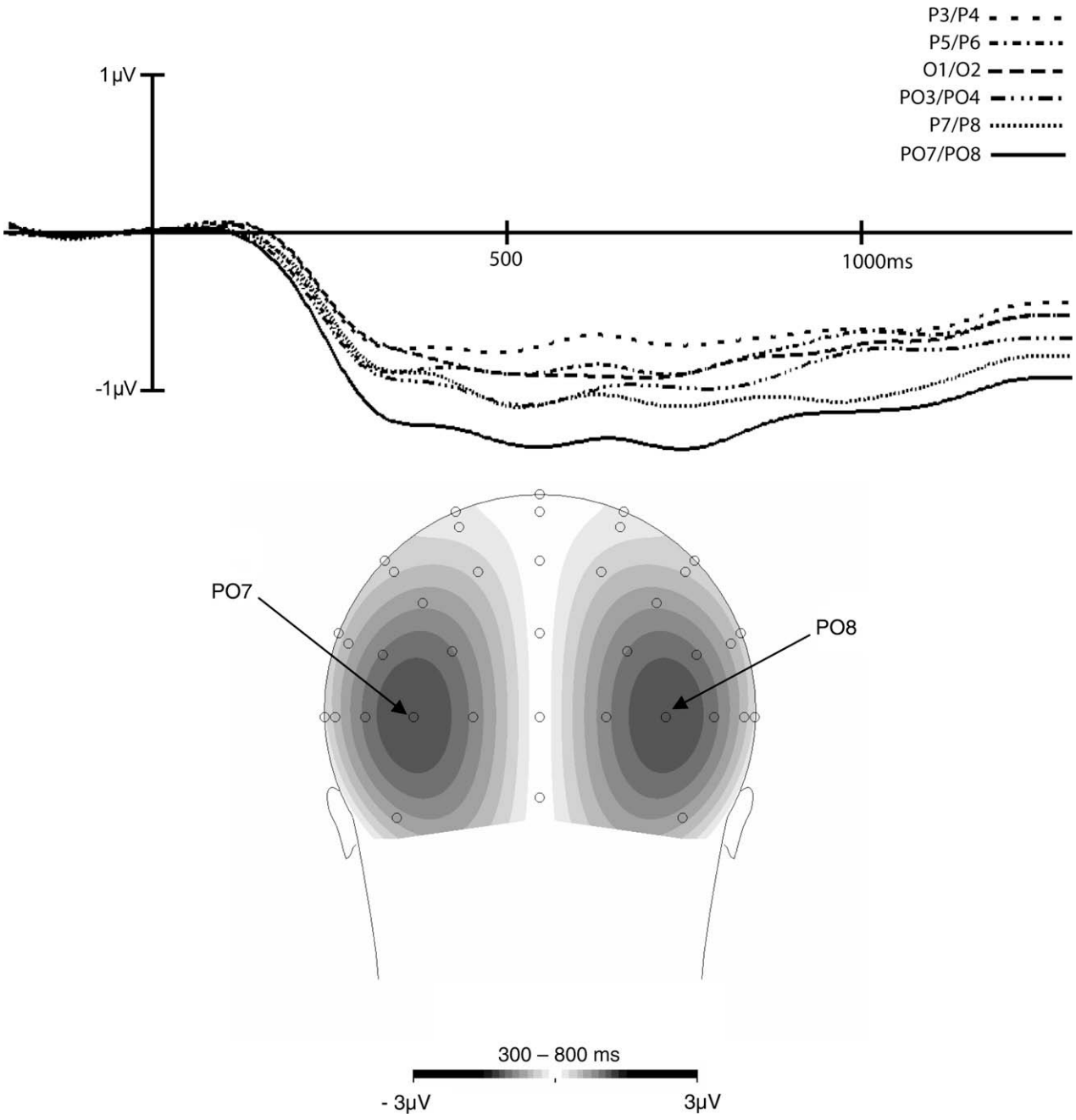

Fig. 3. Top part. SPCN (ipsilateral – contralateral difference) waveforms for posterior electrodes P3/P4, P5/P6, P7/P8, PO3/PO4, PO7/PO8 and O1/O2. Bottom part. Distribution of SPCN mean voltage during the SPCN (300–800 ms), as determined by interpolation of the spherical splines. The waveforms were filtered with a 5 Hz, 48 dB/octave low-pass filter for display purposes only.

the 1200–1300 ms time window (−0.82 μV and −0.72 μV, respectively, $F(1, 34) = 1.37$, $MSE = .41$, $p > .24$). As predicted, activation in below fixation trials started at a larger amplitude than in the above fixation trials. However, amplitude in above-fixation trials did not increase towards the end of the time window, but instead remained stable. This latter pattern probably reflects a growing activation of the lower (below fixation) portion of the curve with time in combination with a general decrease of SPCN amplitude as a greater proportion of trials are completed. Indeed, after 1300 ms, 45% of trials have been completed. Since we expect the SPCN to taper off as curves are no longer being processed, we can expect averaged SPCN amplitude to decrease as more and more trials are completed in both conditions. Thus, in below-fixation starting trials, this tendency towards a decrease in amplitude should add to the amplitude decrease expected when the tracing of curves switches to the upper field. In the above-fixation trials, however, this amplitude decrease could diminish or even cancel out the amplitude increase expected from the switch from tracing in the upper visual field to the lower visual field, and thus explain the pattern of results we observed.

4. Discussion

The process of covert visual curve tracing has been postulated to be an important basic operation, or building block, for more complex visual routines used to analyze, process, and understand complex visual scenes (Ullman, 1984). Given sharp processing

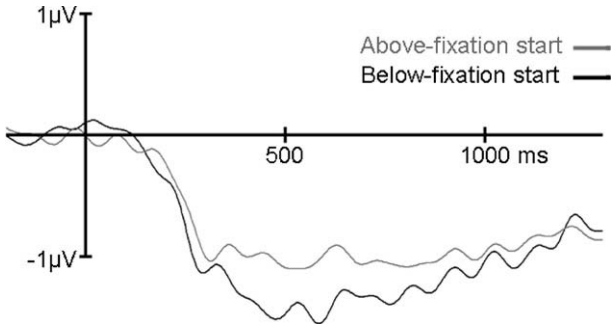

Fig. 4. SPCN (ipsilateral – contralateral difference) waveforms for pooled electrodes PO7/PO8, P7/P8, and PO3/PO4, separately for trials with targets curves starting above fixation (grey line) and target curves starting below fixation (black line). The waveforms were filtered with a 10 Hz, 48 dB/octave low-pass filter for display purposes only.

capacity limitations in later stages of visual processing (Pinker, 1984), mechanisms of selective attention must operate on earlier representations to guide later processing. Curve tracing can be conceptualized as a form of path-guided deployment of visual-spatial selective attention that is naturally engaged in visual scene analysis in everyday life, and which can be isolated by more specialized displays and tasks. In the simple task we devised for the present experiment, an efficient processing strategy consisted of shifting attention to the end of the curve marked by the white circle (Fig. 1) followed by covert tracing of the curve to the other end, followed by the identification and report of the colour of the disk found at that location. Other strategies could be imagined. For example, one could start at one of the coloured disks, trace the curve to the other end, and determine if it terminated at the white circle. If not, one would start at another coloured disk, and the process could be repeated until the correct curve was found. This alternative strategy would be less efficient, however, because on average 2.5 curves would need to be traced in order to find the correct one, whereas starting at the white circle guaranteed a solution after tracing a single curve. Given that the configuration of curves and starting point changed randomly from trial to trial, we expected that participants would engage in curve tracing (e.g., Jolicœur et al., 1986), and that they would use the most efficient strategy available to them (allowing us to predict which curve would be traced).

Most importantly, the curves to be traced traversed visual space either in the left visual field or the right visual field. A differential activation of the cells firing to represent the target curve would thus be expected to cause a lateralized response, with dominance in the contralateral cerebral hemisphere. We observed just such an effect in the form of an SPCN that onset about 180 ms after the onset of the set of curves. This onset latency is remarkably similar to the time at which the firing rates of cells in the visual system of monkeys differentiate between target and non-target curves in a curve tracing task (Roelfsema et al., 1998).

The observed difference in SPCN amplitude for stimuli processed in the upper or lower portion of the hemifield offers interesting evidence supporting the spreading of attention model of curve tracing. They should be interpreted with caution, however. There is a great variability in overall RTs (SD $\approx$ 350 ms). Even assuming speed of tracing to be constant on all parts of a curve (which might not be the case as curvature and the presence of distractor curves can impact on tracing rate), this means that the crossover from above or below fixation to the opposite hemifield might occur at very different moments from one trial to another, and from one participant to another. This, in turn, makes it very likely that there will be a long portion of the waveform that represents an overlap of trials that are being traced before and after the crossover within the same condition. Therefore, it is not entirely impossible that a task where speed of tracing and thus the moment of crossover are controlled better, we might observe a reversal of SPCN amplitude consistent with a spotlight model of curve tracing. Nonetheless, the present evidence (Fig. 4) in which the amplitude of the SPCN is initially larger for trials in which the hypothesized curve-tracing process started below fixation relative to trials on which the process started above fixation, but later converge to a common value, is consistent with a lingering activation of the curve rather than a rapid return to an inactivated state.

An interesting observation is that the tracing-related SPCN appeared quite similar in latency and scalp distribution, as well as in the lower/upper hemifield amplitude differences observed, to the SPCN observed in visual short-term memory tasks (see for example Jolicœur et al., 2008; Perron et al., 2009). This raises the issue of the relationship between visual short-term memory and curve tracing. Our working hypothesis is that both covert curve tracing and the active maintenance of information in visual short-term memory may require enhanced neuronal activity in extra-striate visual cortex, with a stronger response in the hemisphere contralateral to the attended side (Robitaille, Grimault, & Jolicœur, 2009). In fact, we do not believe that the curve tracing task performed by our participants is directly comparable to active maintenance of representations in visual short-term memory. Rather, we interpret the present results as evidence that the SPCN component can also be observed during the active processing of a stimulus present in perception (as were the curves to be traced in the present paradigm). A similar conclusion can be drawn from the SPCN observed during the performance of a multiple object tracking task in which the tracked objects were presented in the left or right visual field (Drew & Vogel, 2008). Whether the brain areas involved in these various tasks that give rise to SPCNs (visual short-term memory, curve tracing, multiple object tracking) are the same, or merely similar is an issue that we cannot resolve on the basis of the present work, and which must be left for future research.

5. Conclusion

In this study, we identified a neurophysiological component of the ERP elicited by covert visual curve tracing in the human brain. Our methods provide a new and powerful way to measure brain activity related to curve tracing, which will be useful in further studies designed to address how the human brain implements visual routines engaged in the processing of complex visual displays. Using this method, we also found supporting evidence for a spread-of-attention model of curve tracing. Additional work using ERPs and extensions of our approach will be needed to understand the relationships between brain activity related to curve tracing, visual short-term memory, and other visual-spatial attentional processes such as those involved in multiple object tracking.

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