Electrophysiological measurement of rapid shifts of attention during visual search

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The perception of natural visual scenes that contain many objects poses computational problems that are absent when objects are perceived in isolation[1]. Vision researchers have captured this attribute of real-world perception in the laboratory by using visual search tasks, in which subjects search for a target object in arrays containing varying numbers of non-target distractor objects. Under many conditions, the amount of time required to detect a visual search target increases as the number of objects in the stimulus array increases, and some investigators have proposed that this reflects the serial application of attention to the individual objects in the array[2,3]. However, other investigators have argued that this pattern of results may instead be due to limitations in the processing capacity of a parallel processing system that identifies multiple objects concurrently[4,5]. Here we attempt to address this longstanding controversy by using an electrophysiological marker of the moment-by-moment direction of attention—the N2pc component of the event-related potential waveform—to show that attention shifts rapidly among objects during visual search.

Behavioural studies of visual search have not conclusively resolved this dispute because they do not provide a moment-by-moment measure of the spatial distribution of attention, making it impossible to determine whether attention shifts rapidly from item to item. In contrast, the N2pc component of the event-related potential (ERP) waveform provides a continuous measure of the distribution of attention by virtue of its lateralized distribution. Specifically, N2pc is a negative-going voltage deflection that is typically observed 200–300 ms after the onset of a visual search array, and it is largest over areas of visual cortex in the hemisphere contralateral to the location of an attended object within the search array. Several experiments have shown that the N2pc component is related to the covert orienting of visual attention before the completion of object recognition[6,7], and further experiments have shown that it reflects a spatial filtering process that closely resembles attention-related modulations of activity measured from cortical neurons in monkeys[8]. Thus, if visual search involves rapid, serial shifts of attention, the N2pc component should shift rapidly between the left and right hemispheres as attention shifts rapidly between the right and left hemifields.

In standard visual search protocols, it is impossible to determine the order in which objects are searched, and this in turn makes it impossible to distinguish between attention-related shifts in the N2pc component and random voltage fluctuations. To solve this problem, we used a modified visual search paradigm in which the subjects were biased to search the objects in a known order. Each search array contained four coloured squares, one in each quadrant, along with 21 black distractor squares (Fig. 1a). The target, a square with a gap on the left side, was present on 50% of trials. To bias the order in which the squares might be searched, we presented the target in one prespecified colour on 75% of the target-present trials and in another prespecified colour on the remaining 25%. We refer to these colours as C_{75} and C_{25}, respectively. For example, to bias a subject to search the red item first and the green item second, the target for that subject was red on 75% of target-present trials and green on 25% of target-present trials. The subjects were informed of the probabilities at the beginning of the session so that they would be familiar with the probability structure. However, they were given no instructions about how to use the probability information (they were not told to search C_{75} first).

Subjects detected the target about 80 ms faster when it was the C_{75} item ($M = 645$ ms) than when it was the C_{25} item ($M = 723$ ms), a statistically significant difference ($P < 0.001$). This result is consistent with both serial and parallel models of attention, but these models make differing predictions concerning the N2pc component. When C_{75} and C_{25} were in opposite hemifields, serial models would predict that the N2pc component would appear first over the hemisphere contralateral to C_{75} and then shift to the hemisphere contralateral to C_{25} (except when the C_{75} item was the target, in which case attention would remain focused on this item). In contrast, typical parallel models would predict that the N2pc component would not switch rapidly between the hemispheres, but would instead be consistently larger over the hemisphere contralateral to C_{75}, owing to a greater allocation of processing resources to this item. Thus, serial models predict rapid interhemispheric switching of the N2pc component whereas typical parallel models predict no change over time.

Figure 1b shows the N2pc component on target-absent trials when C_{75} and C_{25} were in opposite hemifields. As predicted by serial search models, the N2pc was more negative over the hemisphere contralateral to C_{75} from 200–300 ms post-stimulus and then became more negative over the hemisphere contralateral to C_{25} from 300–450 ms post-stimulus. When C_{25} and C_{75} were both in the

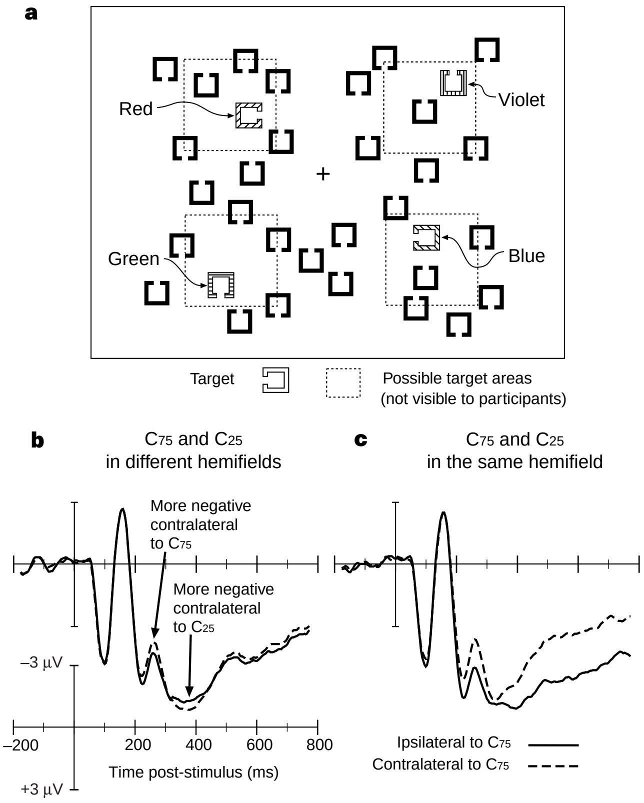

Figure 1 Stimuli and results from the first experiment. **a**, Example visual search array. **b**, ERP waveforms for non-target stimuli at lateral occipital electrode sites when C_{75} and C_{25} were in opposite hemifields, averaged across subjects. The contralateral waveform is an average of the left hemisphere waveform when C_{75} was in the right visual field and the right hemisphere waveform when C_{75} was in the left visual field, and the ipsilateral waveform is an average of the left hemisphere waveform when C_{75} was in the left visual field and the right hemisphere waveform when C_{75} was in the right visual field. **c**, Analogous waveforms when C_{75} and C_{25} were in the same hemifield.

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same hemifield (Fig. 1c), the N2pc remained contralateral to that hemifield until the end of the recording epoch (consistent with both serial and parallel models). Thus, the 80-ms difference in response time between the C_{75} and C_{25} targets was paralleled by a similarly timed shift in N2pc lateralization when C_{75} and C_{25} were in opposite hemifields. These results show that, at least under some conditions, attention shifts rapidly among the non-target items in a visual search array. Moreover, the timing of the shift is comparable to the search rates obtained in behavioural experiments with similarly difficult-to-discriminate targets[9].

To assess these results statistically, N2pc measurements for early (200–275 ms) and late (350–425 ms) time intervals were entered into an analysis of variance (ANOVA) with factors of stimulus configuration (that is, C_{75} and C_{25} in the same versus opposite hemifields), N2pc measurement interval and electrode site. The presence of a polarity reversal between the early and late intervals when C_{75} and C_{25} were in opposite hemifields, but not when they were in the same hemifield, led to a statistically significant interaction between stimulus configuration and N2pc measurement interval ($F[1,9] = 5.68$, $P < 0.05$). Additional analyses confirmed that, when C_{75} and C_{25} were in opposite hemifields, the N2pc effects were significant in both the early and late intervals ($F[1,9] = 8.40$, $P < 0.02$ and $F[1,9] = 5.88$, $P < 0.05$, respectively). In addition, to test whether the early and late phases of the N2pc component in Fig. 1b arose from the same neural generator source, normalized scalp distributions[10] were compared in an additional ANOVA (including only the data from trials in which C_{75} and C_{25} were in opposite hemifields). The interaction between electrode site and N2pc measurement interval in this ANOVA was very far from statistical significance ($F[11,99] = 0.50$, $P = 0.90$), consistent with a common neural generator source.

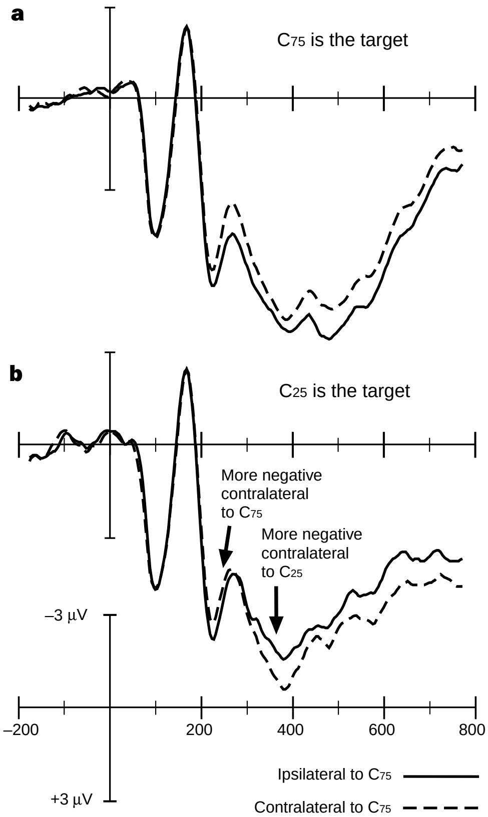

Figure 2 ERP waveforms at lateral occipital electrode sites when C_{75} and C_{25} were in opposite hemifields, averaged across subjects for C_{75} targets (**a**) and C_{25} targets (**b**) in the second experiment.

There were too few C_{25} targets in this experiment to provide an adequate analysis of the target-present trials, and a second experiment was therefore conducted in which a target was present on every trial. Subjects reported whether the target's gap was on the top or bottom of the square (non-targets had a left gap or a right gap). When C_{75} was the target, the N2pc component was more negative contralateral to this item from 200 ms until the end of the recording epoch (Fig. 2a). In contrast, when C_{25} was the target, the N2pc was initially more negative contralateral to C_{75} and then became more negative contralateral to C_{25} (Fig. 2b). This pattern of effects led to a statistically significant interaction between target item (C_{75} versus C_{25}) and N2pc measurement interval ($F[1,9] = 7.77$, $P < 0.02$). Additional analyses confirmed that the N2pc effects for the C_{75} targets were significant in both the early and late intervals ($F[1,9] = 6.49$, $P < 0.05$ and $F[1,9] = 5.33$, $P < 0.05$, respectively). These results indicate that attention was first directed toward C_{75} and, if the visual system determined that this item was not the target, attention was then rapidly redirected toward C_{25}.

It is possible that the probability manipulation that we used to bias the search order in these experiments led subjects to adopt a serial search strategy even though they would ordinarily use a parallel strategy. A third experiment was therefore conducted that did not use an artificial means of biasing the search order but instead took advantage of subjects' pre-existing tendencies to search items near fixation before searching items far from fixation[11,12]. The search arrays in this experiment consisted of 40 black items and 1 or 2 red items, with the red items occurring either near or far from fixation and in the same or opposite hemifields. The target, if present, was always a red item and was equally likely to appear at either eccentricity.

As shown in Fig. 3, when one red item was near fixation and the other was far from fixation and in the opposite hemifield, the N2pc was more negative contralateral to the near item from about 200–300 ms and then become more negative contralateral to the far item from about 300–450 ms. This reversal was not present when the near and far items were in the same hemifield, and these different patterns of lateralization led to a statistically significant interaction between stimulus configuration (near and far items in the same versus opposite hemifields) and N2pc measurement interval ($F[1,9] = 7.72$, $P = 0.02$). Additional analyses confirmed that the N2pc effects shown in Fig. 3 were significant in both the early and late intervals ($F[1,9] = 7.03$, $P < 0.05$ and $F[1,9] = 6.80$, $P < 0.05$, respectively).

This experiment indicates that attention switches rapidly among the non-target items even when no artificial methods are used to

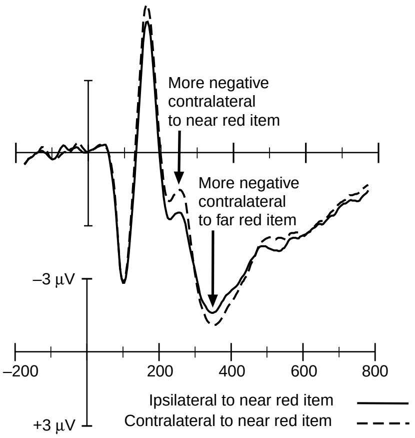

Figure 3 ERP waveforms for non-target stimuli at lateral occipital electrode sites when the near and far red items were in opposite hemifields, averaged across subjects in the third experiment.

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bias the search order, consistent with serial models of visual search. However, this pattern of results could potentially be explained by an intrinsically slower N2pc time course for the far item than for the near item. To rule out this possibility, we included trials with a single red item, and the N2pc on these trials had almost exactly the same time course whether this item was near or far. Thus, the results shown in Fig. 3 cannot be explained by intrinsic differences in the time course of processing for near and far items.

A completely flexible parallel model can emulate any serial model[13], and it is therefore impossible to rule out all parallel search models without also ruling out all serial search models. For example, 75% of processing resources might initially be allocated to the C_{75} item, and when the visual system has determined that this item is not the target, these resources might be rapidly released to the C_{25} item, producing results such as those obtained here. However, the present results do rule out the vast majority of parallel models in which the overall distribution of attention does not shift rapidly among the items in the search array; that is, those that do not approximate a serial search model. Thus, by electrophysiologically tracking the moment-by-moment distribution of attention, we have provided direct evidence that visual search involves rapid shifts in the distribution of attention among objects. □

Methods

Stimulus arrays in the first experiment were presented within a 9.8° × 9.8° region on a light grey background (9.9 cd m^{-2}). Each item within an array subtended 0.72° × 0.72°, with a 0.2° gap on one side, and the items were presented in black, green, red, blue or violet. Arrays were presented for 2,000 ms, followed by a blank interstimulus interval of 800–1200 ms. In the second and third experiments, the sizes of the arrays and the individual items were reduced by 50% to minimize eye movements. In the first two experiments, each quadrant contained 5 or 6 black items and one coloured item, and the assignment of colours to quadrants varied randomly across trials. The specific colours used for C_{75} and C_{25} were randomized across subjects. In the third experiment, 10–11 items appeared in each quadrant, with either one or two red items in the array. When two red items were present, they were in different quadrants, selected at random; one was near fixation (0.6–1.0°) and the other was far from fixation (1.7–2.4°). As in previous studies of eccentricity in visual search, the sizes of the objects in the third experiment were increased at greater eccentricities according to the cortical magnification factor[11,12]. Each subject received one training block and either 10 (first and second experiments) or 12 (third experiment) experimental blocks. Each block contained 104 trials.

ERPs were recorded from 10 neurologically normal college students in each experiment using our standard recording and analysis procedures[7], including rejection of trials contaminated by blinks or large (>1°) eye movements. In addition, signal-averaged electro-oculogram recordings were used to ensure that average eye position did not deviate more than 0.2° toward the target for any subject. The N2pc was measured at occipital, lateral occipital and posterior temporal electrode sites as the difference in mean amplitude between the contralateral and ipsilateral waveforms, with measurement windows of 200–275 and 350–425 ms.

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Global and fine information coded by single neurons in the temporal visual cortex

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When we see a person's face, we can easily recognize their species, individual identity and emotional state. How does the brain represent such complex information? A substantial number of neurons in the macaque temporal cortex respond to faces[1–12]. However, the neuronal mechanisms underlying the processing of complex information are not yet clear. Here we recorded the activity of single neurons in the temporal cortex of macaque monkeys while presenting visual stimuli consisting of geometric shapes, and monkey and human faces with various expressions. Information theory was used to investigate how well the neuronal responses could categorize the stimuli. We found that single neurons conveyed two different scales of facial information in their firing patterns, starting at different latencies. Global information, categorizing stimuli as monkey faces, human faces or shapes, was conveyed in the earliest part of the responses. Fine information about identity or expression was conveyed later, beginning on average 51 ms after global information. We speculate that global information could be used as a 'header' to prepare destination areas for receiving more detailed information.

We recorded the activity of 1,874 single neurons in the inferior temporal cortex, including both banks of the superior temporal sulcus (STS), from A14 to A24, of four hemispheres in two monkeys (*Macaca fuscata*) (Fig. 1a). The monkeys were trained to maintain their gazes while visual stimuli were presented. The test stimuli (Fig. 1b–d) were coloured pictures of 16 monkey faces (4 models with 4 expressions), 12 human faces (3 models with 4 expressions) and 10 geometric shapes (rectangles and circles, each in 1 of 5 colours; brown is not shown in the figure). Of the 1,874 cells, 158 (8%) were face-responsive neurons, responding to at least one of the facial stimuli, of which 86 cells were quantitatively analysed.

As shown in Fig. 1b–d, a single face-responsive neuron responded to all facial stimuli but not to the shapes. Its temporal discharge patterns differed among the facial stimuli. For example, the full open-mouthed face (C) of all monkey models elicited strong and sustained discharges lasting up to 500 ms, whereas the neutral (A) and pout-lips (B) face of all monkey models elicited only the initial transient discharge. To determine how facial information was coded by the neuronal responses, the information was classified into one global and four fine categories. A global category (G) represents

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