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Direct measurement of attentional dwell time in human vision

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In vision, attentional limitations are reflected in interference or reduced accuracy when two objects must be identified at once in a brief display[1,2]. In our experiments a brief temporal separation was introduced between the two objects to be identified. We measured how long the first object continued to interfere with the second, and hence the time course of the first object's attentional demand. According to conventional serial models, attention is assigned rapidly to one object after another, with a dwell time of only a few dozen milliseconds per item[3,4]. But we report here that interference lasts for several hundred milliseconds—an order of magnitude more than the prediction of conventional models. We suggest that visual attention is not a high-speed switching mechanism, but a sustained state during which relevant objects become available to influence behaviour. This conclusion is consistent with recent physiological results in the monkey[5].

Conventional estimates of attentional dwell time are based on measurements of the speed[3,6] or accuracy[4,7] of visual search. If the time taken to detect a target stimulus increases by a few milliseconds for each nontarget added to a display, one interpretation is that attention moves rapidly and serially from one object to another until the target is found[3,6]. Corresponding arguments concern accuracy when displays are brief[4]. However, such data can also be explained by limited-capacity parallel processing models with substantially greater dwell times[8–10]. According to these models, attention can be divided between several objects at once, but with increasing cost as the number of attended objects increases.

To address this ambiguity, we adapted the techniques of visual search to measure directly how long an object that must be identified continues to occupy attentional capacity. As with standard search techniques, we presented several display items at unpredictable locations within a single trial. But rather than presenting display items simultaneously, we presented just two items separated in time. Attention was engaged on the first object by asking for its identification. At varying intervals afterwards, the second object was presented and interference of the first

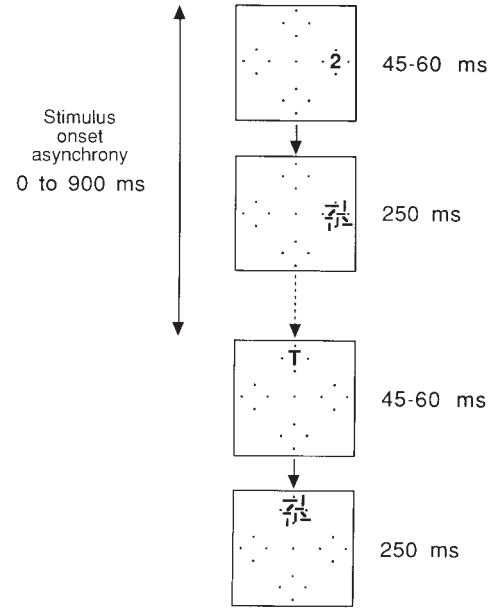

FIG. 1 Events on a single trial. A $5° \times 5°$ fixation display, present at all times, consisted of a central dot and four frames indicating possible stimulus positions. Subjects initiated the trial by pressing a key; one character was presented after a random delay of 0–500 ms, and a second after a further delay of 0–900 ms, measured from onset to onset (stimulus onset asynchrony, or SOA). One of these characters was a green digit (2 or 5), appearing in one of the horizontal locations (left or right frame). The other was a red letter (L or T), appearing in one of the vertical locations (top or bottom frame). The order of these two was unpredictable. Characters measured $0.5° \times 0.6°$, and were presented for 45–60 ms (average 57 ms), as determined for each subject in an initial series of at least 60 calibration trials. Each character was immediately followed by a 250-ms masking pattern used to limit visual persistence. In a testing session, there were three blocks of 156 trials each, given in counterbalanced order. These corresponded to three types of reports: subjects were instructed to identify just the green digit (ignore vertical locations), just the red letter (ignore horizontal locations), or both characters. Subjects pressed keys to indicate their responses, and responses were always withheld until both characters had been presented. Feedback (overall percent correct) was given at the end of each block. Nine subjects (mean age 33) participated in two sessions each.

object on the second was measured as a function of temporal separation. This method tracked continuously in time the attentional demands of first object identification.

On each trial of our first experiment (Fig. 1), two alphanumeric characters were presented, a green digit and a red letter. Each character was presented for only 45–60 ms, with an unpredictable interval of 0–900 ms (measured from onset to onset) between the two. When both characters were to be identified (Fig. 2; filled circles), the one coming second suffered prolonged interference. Indeed, at separations of 100–300 ms, the second character was identified even less accurately than characters presented simultaneously. This should be expected if attention is divided equally between characters with simultaneous presentation, but focused on the first character when presentation is asynchronous. Interference gradually declined at separations greater than 300 ms. In contrast, performance was independent of temporal separation when only one character was identified and the other ignored (Fig. 2; open circles). Measured directly by this method, identifying an object occupies attention for at least several hundred milliseconds.

To rule out the possibility that this estimate of attentional dwell time might depend upon the requirement to make independent, overt responses to each character, we adapted our methods more closely to visual search, so that the task was simply to detect the presence of a target among non-targets. The two characters presented on each trial were both Ls, presented either upright (target) or rotated 90° clockwise or anticlockwise (non-targets). After each trial the observer indicated with a single response whether a target had been seen. Results were very much as before. When the first character was a non-target, a subsequent target suffered prolonged interference (Fig. 3).

A different aspect of attentional dynamics is the time taken to respond to a cue indicating how attention should be directed: for example, which items in a display should be reported[11,12]. Such measurements reflect the time needed to identify the cue, to determine its meaning, and to establish the appropriate selection rule. In our experiments there was no instructional cue to be interpreted. As in conventional visual search, the subject simply had to identify the separate display items. We have shown that processing a single item in a visual search or identification task occupies attentional capacity for several hundred milliseconds.

In further experiments we obtained similar estimates of dwell time under a variety of different conditions. Increasing the complexity and duration of response processes for the first object had no effect, differentiating the interference measured here from delays in response processing known by convention as the 'psychological refractory period'[13]. We also obtained similar estimates of dwell time when objects appeared successively at fixation instead of at different spatial locations. The time we measured is concerned not with shifting attention from one location to another in the visual field, but with how long an object that must be identified continues to occupy attentional capacity. Indeed, an extended attentional dwell time helps explain the results of previous experiments using rapid sequences of many characters, presented one after the other at a single location[14,15]. Finally, if the first display contained two relevant characters rather than one, interference with the second display was strengthened, reflecting increased division of attentional capacity.

Conventional visual search results can be explained either by high-speed serial models or limited-capacity parallel models of visual attention. By measuring attentional dwell time directly, we have shown that high-speed serial models are incorrect. Instead, we suggest attention to a relevant object is a sustained

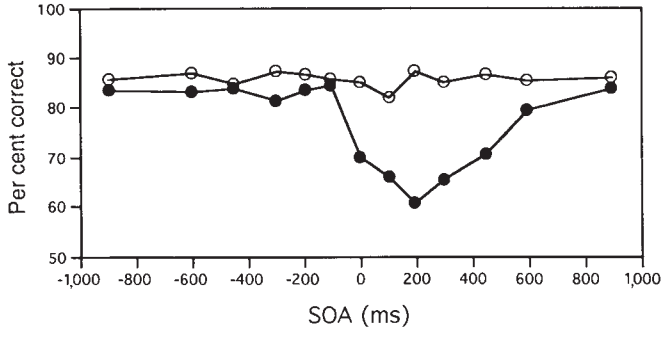

FIG. 2 Results from experiment 1. The figure shows accuracy of target identification either when both characters were attended (filled circles) or when one could be ignored as it appeared in an irrelevant location (open circles). Negative SOAs refer to the item presented first in the trial and positive SOAs refer to the item presented second. Performance varied little between testing sessions, or on letters versus digits; the figure averages over these variables. When both characters were attended, the second suffered interference at temporal separations at least up to 450 ms. As compared to asymptote (estimated by mean accuracy at maximal temporal separation), accuracy was significantly reduced at each SOA between 0 and 450 ms ($P<0.004$ or better in each case, t-test). In this experiment there was no interference from a stimulus that could be ignored (conditions in which subjects ignored either horizontal locations (green digits) or vertical locations (red letters)). For these conditions (open circles), data for the single character identified are plotted as a function of SOA with respect to the ignored character. In other experiments mild interference sometimes remains in this case, suggesting that even a character in an ignored location has some tendency to attract attention to itself[18].

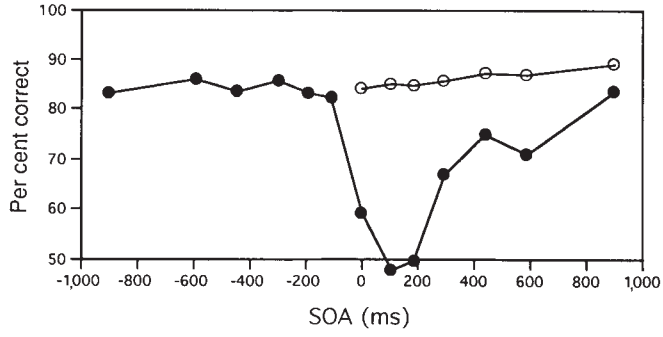

FIG. 3 Results from experiment 2. Two characters were presented as before, one in the left or right display frame and one in the top or bottom frame. Stimulus exposure durations ranged from 40–104 ms (average 73 ms); SOAs and other details were as before. Each character was a letter L, measuring $0.6° \times 0.6°$, presented either in its normal upright orientation (target) or rotated 90° clockwise or anticlockwise (non-targets). A single target, either the first or the second character to appear at random, was present on 50% of the trials. The subject's task was to indicate whether or not a target had appeared by pressing a key at the end of the trial. Data presented come only from a condition in which both characters were attended, because the target could appear in any display location. For target-present trials (filled circles), data have been separated into negative (target presented first) and positive (target presented second) SOAs. Target detection was substantially impaired by a preceding non-target, up to temporal separations of at least 300 ms (differences from asymptotic accuracy significant at each SOA between 0 and 300 ms, $P<0.001$ in each case), and probably longer ($P<0.06$ at SOA of 450 ms; $P<0.02$ at SOA of 600 ms). For trials with no target, SOAs cannot be defined as negative or positive; data (open circles) are shown simply as a function of temporal separation between the two non-targets. For these trials, accuracy was virtually independent of SOA, showing that interference at short SOAs was reflected almost entirely in missed targets rather than false positives. As before, conditions in which one character could be ignored, because its display location was known to be irrelevant, showed much attenuated interference (data not shown). Data come from 24 subjects (mean age, 34), each participating in a single session.

state, during which that object is available to awareness for the control of behaviour. Although largely independent of eye movements[16], attention has a comparable dwell time. This conclusion is consistent with recent neurophysiological data. In the high-level visual cortex of the monkey, attention is reflected in part by suppression of neuronal responses to ignored objects[5,17]. This suppression develops over several hundred milliseconds (ref. 5), as does the interference with subsequent inputs shown here in behaviour. □

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Translational regulation of *nanos* by RNA localization

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LOCALIZATION of the maternally synthesized *nanos* (*nos*) RNA to the posterior pole of the *Drosophila* embryo provides the source for a posterior-to-anterior gradient of Nos protein[1,2]. Correct spatial regulation of *nos* activity is essential for normal pattern formation. High local concentrations of Nos protein in the posterior of the embryo are necessary to inhibit translation of the transcription factor Hunchback in this region[3,4], and thus permit expression of genes required for abdomen formation (see ref. 5 for review). By contrast, misexpression of Nos protein at the anterior of the embryo prevents translation of the anterior morphogen Bicoid, suppressing head and thorax development[1,6–9]. Posterior localization of *nos* RNA is mediated by sequences within the *nos* 3′ untranslated region (3′UTR)[1] and requires the function of eight genes of the 'posterior group'[2,6]. Although the unlocalized *nos* RNA is stable in embryos from females mutant for any of the posterior group genes, these embryos appear to lack *nos* activity because they develop the abdominal defects characteristic of embryos produced by *nos* mutant females[2,6,10–14]. We report here that unlocalized *nos* RNA is translationally repressed. Translational repression is mediated by the *nos* 3′UTR and can be alleviated either by replacement of the 3′UTR with heterologous 3′UTR sequences or by posterior localization. Thus, RNA localization provides a novel mechanism for translational regulation.

nos RNA localization requires the activity of at least eight posterior group genes including *oskar* (*osk*) and *vasa* (*vas*)[2]. Embryos produced by females mutant for these genes fail to localize *nos* RNA but contain wild-type levels of this RNA[2] (Fig. 1*a*). To determine whether the lack of *nos* function in these embryos results from failure to generate a concentrated source of Nos protein or from lack of Nos protein altogether, we analysed Nos protein in extracts of embryos from wild-type and mutant females. Nos protein was not detected in extracts of embryos from osk^- or vas^- females (Fig. 1*b*). Thus, the similarity of phenotype between embryos from osk^- or vas^- females and embryos from females carrying a null *nos* mutation results from the lack of Nos protein. This suggests that unlocalized *nos* RNA is translationally inactive and that this translational inhibition is relieved by RNA localization. A link between RNA localization and translation is further supported by the finding that an increase in the *osk* gene dosage from 2 copies (wild-type females) to 4 copies ($4 \times osk^+$ females) results in an increase both in the amount of *nos* RNA localized to the posterior of the embryo[15,16] and in the amount of Nos protein produced (Fig. 1*b*), whereas the total *nos* RNA level remains constant (Fig. 1*a*). This suggests that *osk* is limiting for *nos* RNA localization and translation.

Because *nos* RNA localization depends on the *nos* 3′UTR, we tested whether translational regulation of *nos* RNA is also meditated through 3′UTR sequences. To determine whether translational repression of unlocalized *nos* RNA requires the *nos* 3′UTR, we constructed a hybrid gene in which the *nos* 3′UTR

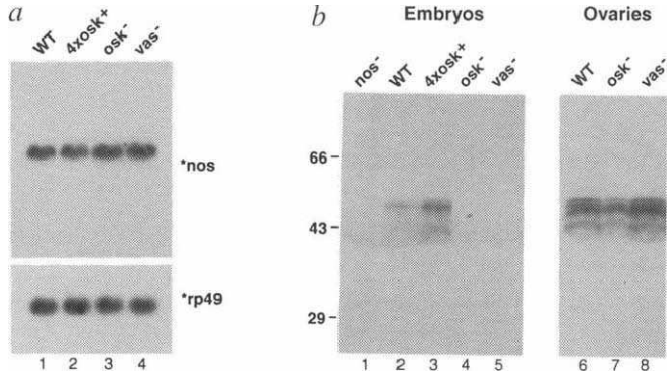

FIG. 1 Effects of posterior groups genes on *nos* RNA and protein levels. *a*, Northern blot analysis of total RNA from 0–2 h embryos from females of the following genotypes: WT (wild-type); $4 \times osk^+$ (4 copies of the wild-type *osk* gene[15]); osk^- (osk^{54}/osk^{84}; refs 11, 22), vas^- (vas^{PD}/vas^{D1}; refs 6, 12). The blot was hybridized sequentially with probes for *nos* RNA (*nos) and for rp49 RNA (*rp49) for standardization. Phosphoimage quantification of the blot revealed that equivalent amounts of *nos* RNA are present in embryos of each genotype. *b*, Immunoblots of extracts from 0–2-h embryos and ovaries. Equivalent amounts of extract of each genotype, as determined by Ponceau-S staining of the blots, were fractionated on 10% SDS–polyacrylamide gels. Nos protein was detected with an anti-Nos polyclonal antibody[2]. No immunoreactive material is present in embryos from null nos^- females (nos^{BN}; ref. 2). Nos protein appears as a set of bands in embryos and ovaries from WT females. The same bands are present in ovaries from osk^- and vas^- females but not in embryos from these mutants. Embryos from $tudor^-$ and $valois^-$ females show reduced amounts of Nos protein (data not shown); the mutant alleles of these genes are most probably not null, however, and permit some *nos* RNA localization[2]. Relative molecular mass markers: BSA, 66K; ovalbumin, 43K; carbonic anhydrase, 29K.
METHODS. *a*, Northern blotting as in ref. 1, using 5 μg total RNA. ^{32}P probes were synthesized from the pN5 cDNA (*nos*; ref. 17) and the ~600 bp *Eco*RI–*Hin*dIII fragment of HR0.6 (rp49; ref. 23). *b*, Ovaries from virgin females fed for 2 days at 25 °C were dissected into EBR[24] and washed with PBS. 0–2 h embryos were collected at room temperature, dechorionated with 50% Chlorox, and washed with dH_2O. Both tissues were frozen in liquid N_2 and stored at −80 °C. Frozen tissues were homogenized in boiling sample buffer (0.125 M Tris-HCl pH 6.8, 4% SDS, 10% 2-mercaptoethanol, 20% glycerol, 5M urea) and boiled for 3 min. Supernatants were separated by SDS–PAGE followed by transfer to nitrocellulose. Immunoblotting with the anti-Nos antibody according to ref. 25, supplementing with 5% calf serum.