Speeding Up Reaction Time with Invisible Stimuli

Silvia Savazzi and Carlo A. Marzi[1]
Department of Neurological and Visual Sciences
Physiology Section
University of Verona
8 Strada Le Grazie
37134, Verona
Italy

Summary

Normal subjects react more quickly to a pair of visual stimuli than to a stimulus alone. This phenomenon is known as the redundant signal effect (RSE) [1] and represents an example of divided visual attention in which signal processing is carried out in parallel to the advantage of response speed. A most interesting aspect of this phenomenon is that it can occur when one stimulus in a pair cannot be consciously detected because of hemianopia [2, 3] or unilateral extinction [4] resulting from brain damage. Here, we report that a similar dissociation between visual awareness and visually guided behavior is present in normal subjects who show an RSE even when the luminance of one of a pair of stimuli is below detection threshold. The observed RSE cannot be attributed to probability summation because it violates Miller's race inequality [5] and is likely to be related to neural summation between supra- and subthreshold stimuli. Given that a similar implicit RSE is present in hemispherectomy patients [3], we hypothesize that the site of this summation might be the superior colliculus (SC).

Results and Discussion

Various implicit visual effects, i.e., those effects that occur without the subjects' perceptual awareness, have been described in the literature [6–10]. Here, we provide novel evidence that a stimulus whose luminance is below the detection threshold can still yield an observable effect on visually guided behavior. Subjects were asked to press a key as quickly as possible following the presentation of single or double small luminous squares briefly presented on a PC screen without having to discriminate between them. There were three degrees of stimulus luminance as determined by previous individual threshold assessment; see Table 1.

Suprathreshold stimuli were set at a luminance that represented the minimum value at which the stimuli could be detected by all subjects in at least 99% of the presentations; as can be seen from Table 1, this value was 0.30 cd/m^2 for all subjects. Subthreshold stimuli were those that were detected in less than 1% of the presentations; their luminance value was 0.05 cd/m^2 for nine subjects and 0.04 cd/m^2 for the remaining three subjects. Finally, control stimuli had such a low lumi-

[1]Correspondence: carloalberto.marzi@univr.it

nance (0.02 cd/m^2) that they were never detected. The various combinations of stimulus number and luminance were alternated in random series.

Figure 1A shows the reaction time (RT) data. Double suprathreshold stimuli yielded reliably faster RTs (356.6 ms) than single suprathreshold stimuli (372.8 ms), with a redundancy gain, that is, with a difference between the mean RT to double and single stimuli of 16.2 ms, and this represents a further confirmation of the RSE.

The novel finding was the occurrence of a reliable RSE even when the double stimulus included a subthreshold component and was therefore perceived as a single stimulus. These mixed double stimuli yielded a mean RT (367.0 ms) that was reliably shorter than that for single suprathreshold stimuli (372.8 ms), with a redundancy gain of 5.8 ms. Finally, when double stimuli were made up of the combination of a control and a suprathreshold stimulus, there was no RSE (single stimuli = 372.8 ms; double = 373.2 ms; redundancy gain = −0.4 ms), and this rules out any artifactual explanation of the implicit effect found.

It should be remarked that a very small minority (about 1%) of subthreshold stimuli were responded to during RSE testing. These RTs were considered errors and were eliminated from analysis. However, it could be argued that a similar proportion of those subthreshold stimuli that constituted the mixed double stimuli could have been detected and could have contributed to the implicit RSE effect. Converse to this possibility, however, is the fact that detected subthresholds stimuli yielded very slow mean RTs, namely, 620 ms for single and 630 ms for double stimuli. Given that single suprathreshold stimuli yielded a mean RT of 373 ms and double suprathreshold stimuli yielded a mean of 357 ms, it is unlikely that the few possibly detected subthreshold stimuli might have contributed to speeding up the RT of double mixed stimuli and therefore to the implicit RSE observed.

All the same, to check this possibility further, we eliminated the fastest RTs in those subjects who responded to subthreshold stimuli. Following this procedure, we recalculated the RSE and carried out the same statistical analyses as before. We found an almost identical and statistically reliable implicit redundancy gain (5.2 ms), and therefore the possibility that the observed RSE was related to subthreshold stimuli that might have been possibly detected was definitively ruled out.

We then tried to assess whether the observed RSE was related to neural [5] or to probability summation [11]. The latter hypothesis posits that the RSE results from a race between independently processed redundant stimuli: the faster stimulus "wins" and triggers the motor response. Thus, the mean of the distribution of RTs to double stimuli will be less than the lesser of the means of the distribution of RTs to single stimuli. The alternative hypothesis is based on a coactivation model [5] postulating that the redundant signals are combined in an activational pool before reaching the threshold for triggering the motor response. Thus, double stimuli

Table 1. Individual Percentage of Detections as a Function of Stimulus Luminance

Luminance (cd/m^2)	Subjects											
	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12
0.58	100	100	100	100	100	100	100	100	100	100	100	100
0.47	100	100	100	100	100	100	100	100	100	100	100	100
0.37	100	100	100	100	100	100	100	100	100	100	100	100
0.30	100	100	100	100	100	100	100	100	100	100	100	100
0.22	98	93	97	98	98	95	93	95	97	95	97	97
0.16	95	92	95	98	98	90	90	90	92	93	93	95
0.11	47	45	47	47	45	45	45	45	47	43	45	45
0.05	0	0	0	0	0	0	0	1.7	1.7	0	1.7	0
0.02	0	0	0	0	0	0	0	0	0	0	0	0

reach the threshold for triggering a motor response faster than single stimuli because of summation effects. We used the method proposed by Miller [1, 5] (race inequality test) to discriminate between the two hypotheses. Miller's inequality sets an upper limit for the cumulative probability of a response given redundant signals. If the upper bound is violated, one can say that the observed RSE is likely to be related to a neural summation; if not, a statistical facilitation effect is probable. For further details on the procedure and on the rationale of the method, see [1, 5]. Figure 1B shows that, for both the redundancy gain observed with double stimuli perceived as such and for that observed with double stimuli perceived as a single stimulus, there is a violation of the race model; hence, a probabilistic explanation can be ruled out.

Once it has been established that a neural coactivation mechanism is a likely possibility to explain our explicit and implicit RSE, an important question arises concerning the information-processing level at which coactivation takes place. One possibility is that coactivation occurs at a center that summates across the intensities of the various stimuli in the display and triggers a faster response for higher than for lower overall intensities; see [12] for a broadly similar hypothesis to explain intersensory facilitation in reaction time. In our Experiment 1, the overall luminous intensity of the display is higher for double than for single stimuli, and therefore the RSE would be explained by a higher activation of the summation center. An alternative possibility is that this center is sensitive to *numerosity* rather than to overall luminous intensity. In this case, two stimuli whose luminous intensity is lower than that of a single stimulus would still show an RSE.

To verify these possibilities, we carried out a second experiment in which the RSE was tested with double stimuli whose summed luminance was either equal to or smaller than that of single stimuli. The results are shown in Figure 2.

We again found an RSE when comparing single stimuli with all three double-stimulus conditions; see Figure 2A. It is important to stress that the redundancy gain (4 ms) found for the comparison between single and mixed double stimuli (95%–5%) represents a further confirmation of the implicit RSE found in Experiment 1 with stimuli of different luminance and in different subjects. Furthermore, application of Miller's inequality showed that, as for Experiment 1, the observed redundancy gains were likely to be related to a coactivation effect; see Figure

2B. The results of Experiment 2 rule out the possibility that the RSE might be explained by a center sensitive to overall luminous intensity. Therefore, it is likely that the RSE is mediated at a level at which stimulus numerosity rather than intensity is taken into account to produce an RSE.

Taken together, these results demonstrate that there are different thresholds for conscious stimulus detection (0.13 cd/m^2) and for unconscious visually guided behavior such as the redundancy gain (between 0.05 cd/m^2 and 0.02 cd/m^2), and this poses interesting questions regarding the neural substrate of conscious versus unconscious visual processing by showing that the latter is more sensitive to luminance.

One potential problem whenever one is confronted with implicit effects is that threshold (or perimetric) assessment and testing of the perceptual effect under investigation might induce different performance strategies in the subjects. For example, one might be more conservative during threshold (or perimetry) testing than during the specific task under investigation [13]. This might produce a spurious implicit effect. This criticism, however, does not apply to the present study, since we used a similar paradigm for both threshold assessment and for RSE testing; see the Experimental Procedures section. It could also be argued that introduction of a "commentary" key such as that used in monkeys by Cowey and Stoerig [14] might have been a more straightforward method to test for implicit effects. This method has its own drawbacks, however, since introducing a secondary task is likely to affect the speed of RT in the primary task (RSE paradigm). Thus, in our present experiments, simple RT to single or double stimuli would have certainly been slowed by the subsequent requirement of deciding whether the stimuli were one or two. This might have changed the likelihood of finding an RSE in the primary task. In light of this possibility, we decided to keep the paradigm as simple as possible and to avoid use of a commentary key.

What might be a likely neural site for the implicit effect observed? A previous study has shown that hemispherectomy patients [3], i.e., patients who lack the primary visual cortex as well as most of the cortical mantle of one hemisphere, show an RSE despite the fact that one stimulus of a pair is presented to the hemianopic hemifield and therefore is not consciously detected. In light of this evidence, a likely possibility is that the RSE might occur at the level of a subcortical visual center such as the SC. This evidence is reinforced by other

A

Speed of Response
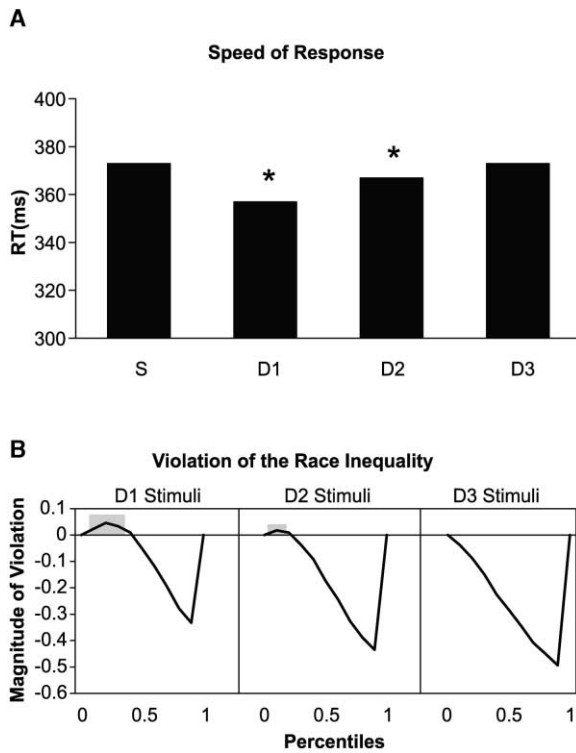

B

Violation of the Race Inequality

Figure 1. Experiment 1: Redundancy Gain and Race Inequality Violation

(A) Mean RTs in the four conditions of stimulus presentation of Experiment 1. S = single stimuli suprathreshold; D1 = double stimuli in which both stimuli are suprathreshold; D2 = double stimuli in which one stimulus is suprathreshold and the other is subthreshold; D3 = double stimuli in which one stimulus is suprathreshold and the other is a control stimulus of very low luminance. The asterisks indicate statistically significant differences between single and double stimuli. The statistical reliability of the differences between single stimuli and double stimuli was assessed by means of a one-way ANOVA for repeated measurements with four levels: S, D1, D2, D3. The ANOVA was highly significant: $F_{(3,33)}$ = 70.065, $p < 0.001$. Post-hoc comparisons were performed with Bonferroni correction and showed a significant advantage of D1 over S ($p < 0.001$) as well as of D2 over S ($p < 0.001$). Finally, D3 was not significantly different from S.

(B) Violation of the race inequality test for the three double-stimulus conditions in Experiment 1. Gray rectangles show the area in which the distributions are significantly different from zero, as assessed by one-sample t tests. The D3 condition did not yield an RSE, and therefore there was no race inequality violation.

A

Speed of Response
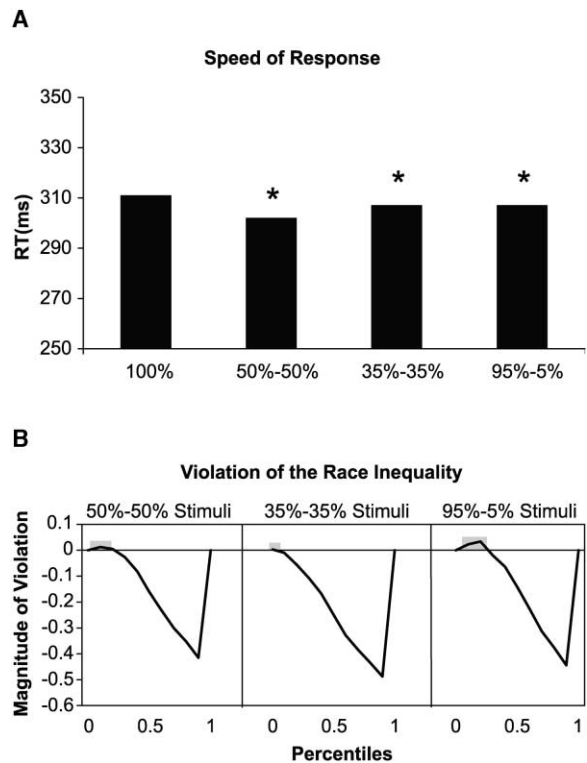

B

Violation of the Race Inequality

Figure 2. Experiment 2: Redundancy Gain and Race Inequality Violation

(A) Mean RTs in the four conditions of stimulus presentation of Experiment 2: single stimuli (100%); double stimuli with luminance of 50%–50%; double stimuli with luminance of 35%–35%; and double stimuli with luminance of 95%–5%. The asterisks mark significant differences between the single stimulus conditions and the others. As for Experiment 1, statistical significance was assessed by a one-way ANOVA, with four levels corresponding to the above-mentioned conditions of stimulus presentation. The ANOVA was highly significant: $F_{(3,33)}$ = 20.170, $p < 0.001$. Post-hoc tests with Bonferroni correction showed that RTs to double stimuli 50%–50% were faster than single stimuli, $p < 0.001$; the same was true for double stimuli 35%–35%, $p < 0.01$ and for double stimuli 95%–5%, $p < 0.001$.

(B) Violation of the race inequality test for the three double-stimuli conditions in Experiment 2. Gray rectangles show the area in which the distributions are significantly different from zero, as assessed by one-sample t tests.

results. First, large redundancy gains have been classically described with multimodal (auditory and visual) stimuli [12], and the SC is a center in which neurons respond to multimodal stimuli [15]. Second, a recent functional magnetic resonance imaging (fMRI) [16] study has shown that the RSE might be mediated by the SC under modulatory influences from the extrastriate cortex. Third, in a previous report, we have provided event-related potential (ERP) evidence that the neural coactivation underlying the RSE might take place at the level of extrastriate cortex [17], an area richly interconnected with the SC. Fourth, other studies [18–20], including our own recent study using a RSE paradigm in conjunction with a stop-signal paradigm [1], have provided evidence

ruling out a motoric stage. On the whole, the picture emerging from these results reinforces the idea that, when visual processing is mainly subserved by a subcortical structure, it remains unconscious. Our present experiments indicate that the SC presumably has a lower threshold for the visual activation of its neurons than visual cortical areas, and this is an important result that bears on the general problem of the neural correlates of conscious experience. A broadly similar question has been posed about the resolution of spatial frequencies. Visual after-effects that are likely to be subserved by cortical neurons show a lower spatial resolution than thalamic neurons in the monkey [21], and this justifies the observation in humans that orientation-selective adaptation and tilt after-effects can be elicited by invisible stimuli [7]. Why should the cortex be less sensitive to low luminance than the SC? One possibility

is that the visual cortical system has adapted for operations such as object and color vision that require an adequate degree of luminance. To reduce overall visual noise, the visual cortex might impose a block on low-luminance signals. In contrast, subcortical centers mediate phylogenetically ancient responses to luminance changes, and it is advantageous for them to have lower luminance thresholds. The cost to pay is the lack of visual awareness.

Experimental Procedures

A total of 12 healthy right-handed subjects (6 males) with normal or corrected-to-normal visual acuity (age range: 19–26 years) took part in the first experiment, and a different group of 12 healthy right-handed subjects (7 males) with normal or corrected-to-normal visual acuity (age range: 19–24 years) took part in the second experiment. All subjects had no history of neurological disease. They gave their informed consent prior to the beginning of the experiments.

The subjects were seated in front of a PC screen with their eyes 57 cm from the center of the screen. A 2000 Hz acoustic warning stimulus (200-ms duration) prompted the subjects to maintain steady fixation and to press the space bar of the PC keyboard with the index finger of their right hand as quickly as possible following the appearance of either a single or double stimulus. The interval between the acoustic warning stimulus and the visual stimulus was randomized within the temporal window of 800–1200 ms. Eye movements were controlled by means of an infrared TV camera placed in front of the subjects. One subject was discarded prior to formal testing because of poor fixation. However, all subjects included in the study had a very stable fixation. This is almost the rule in a simple RT task and with unstructured light stimuli presented in the near retinal periphery. In such conditions, the urge to try and foveate the stimuli is very small.

The range of accepted RTs was 120–850 ms; trials with shorter or longer RTs were a minuscule minority and were not entered in the analyses. The number of omission or commission errors was negligible, in keeping with the easiness of the task. The stimuli used for both threshold assessment and for the two RSE experiments were squares of about $1°$ diameter. They were presented on a video monitor with an exposure duration of 150 ms and at an eccentricity of $6°$ along the horizontal meridian either to the right or to the left of the fixation point in an unpredictable sequence. The background luminance was 0.001 cd/m^2. The subjects were dark adapted for 5 min prior to testing.

The luminance values of the stimuli used (see Table 1) were so low that our photometer (Tektronix J1820) could not measure them. Therefore, we used an indirect method as follows: with the photometer, we measured the luminance on the monitor screen (Nec/Multisync 5D) of nine stimulus intensities (ranging from 47.18 cd/m^2 to 1.34 cd/m^2) corresponding to the codes specified by the commercial software used to generate the stimuli and to run the experiment (MEL2, Psychology Software Tools). We then calculated the power function best fitting the measured values (R^2 = 0.9945) and extrapolated from that function the luminance values of the stimuli whose intensity was not directly measurable.

Experiment 1 consisted of two parts. In the first part, the subjective detection thresholds were assessed for each subject by using the method of constant stimuli (range of luminance: 0.02–0.58 cd/m^2). In the second part, subjects underwent RSE testing.

Stimuli and general procedure were the same for threshold assessment and RSE testing with the difference that, in the former, only single stimuli were used. Moreover, the dependent variable was the percentage of correct detections for threshold assessment and the RT for RSE testing. For threshold assessment, the stimuli had nine different luminance values ranging from 0.02 cd/m^2 to 0.58 cd/m^2. There were six blocks: on each block, each luminance value was presented five times to the right and five times to the left hemifield. The sequence of luminance values and of right-left presentations was randomized. Each luminance value, therefore, was presented 60 times overall. The total number of stimulus presenta-

tions for each subject was 540. The subject's task was to press the space bar of the PC when a stimulus was detected and to refrain from pressing when the stimulus was not detected. For each subject, a psychophysical function was determined and the absolute threshold was taken as the luminance value at which there were 50% detections; see Table 1 for the percentage of detections for individual subjects. The psychophysical function was obtained by transforming the proportion of detection into z scores. With the least-squares method, we assessed the best fitting linear function and the luminance value yielding 50% detection (0.13 cd/m^2) corresponding in the ordinates to z = 0. For RSE testing, each subject received a total of 720 stimuli divided into 13 combinations as follows: 120 suprathreshold single stimuli, half to the right and half to the left hemifield in a randomized balanced sequence; 60 subthreshold single stimuli and 60 control single stimuli, half to the right and half to the left; 120 suprathreshold double stimuli; 120 double mixed supra- and subthreshold stimuli and 120 double mixed suprathreshold and control stimuli (the weaker stimulus in the pair was presented either to the right or to the left in a balanced randomized sequence); 60 double subthreshold and 60 double control stimuli. RTs to single or double subthreshold stimuli were, as pointed out in the text, only a tiny minority. There were no responses to single or double control stimuli.

In Experiment 2, there were four conditions of stimulus presentation: single stimuli (either right or left) with a luminance of 1.04 cd/m^2; double stimuli, with each stimulus in a pair having a luminance of 50% with respect to the single stimulus condition; double stimuli, with each stimulus in a pair having 35% luminance with respect to the single stimulus condition; and a mixed condition in which one stimulus in a pair had 95% of the luminance of the single stimulus (0.99 cd/m^2) and the other had only 5% (0.05 cd/m^2) and, as a consequence, was detected less than 1% of the time, as for subthreshold stimuli in Experiment 1. The total number of trials was 480 subdivided as follows: 120 single stimuli (half to the right and half to the left); 120 double 50%–50% stimuli; 120 double 35%–35% stimuli; 120 double 95%–5% (half with the weak stimulus to the right and half with the weak stimulus to the left). The range of accepted RTs was 120–650 (the cutoff for slow RTs was shorter than for Experiment 1, in consideration of the overall faster speed of response).

References

1. Cavina-Pratesi, C., Bricolo, E., Prior, M., and Marzi, C.A. (2001). Redundancy gain in the stop-signal paradigm: implications for the locus of coactivation in simple reaction time. J. Exp. Psychol. Hum. Percept. Perform. 27, 932–941.

2. Marzi, C.A., Tassinari, G., Aglioti, S., and Lutzemberger, L. (1986). Spatial summation across the vertical meridian in hemianopics: a test of blindsight. Neuropsychologia 24, 749–758.

3. Tomaiuolo, F., Ptito, M., Marzi, C.A., Paus, T., and Ptito, A. (1997). Blindsight in hemispherectomized patients as revealed by spatial summation across the vertical meridian. Brain 120, 795–803.

4. Marzi, C.A., Smania, N., Martini, M.C., Gambina, G., Tomelleri, G., Palamara, A., Alessandrini, F., and Prior, M. (1996). Implicit redundant-targets effect in visual extinction. Neuropsychologia 34, 9–22.

5. Miller, J. (1982). Divided attention: evidence for coactivation with redundant signals. Cognit. Psychol. 14, 247–279.

6. Bonneh, Y.S., Cooperman, A., and Sagi, D. (2001). Motion-induced blindness in normal observers. Nature 411, 798–801.

7. He, S., and MacLeod, D.I. (2001). Orientation-selective adaptation and tilt after-effect from invisible patterns. Nature *411*, 473–476.

8. Kunst-Wilson, W.R., and Zajonc, R.B. (1980). Affective discrimination of stimuli that cannot be recognized. Science *207*, 557–558.

9. MacLeod, D.I., and He, S. (1993). Visible flicker from invisible patterns. Nature *361*, 256–258.

10. Meeres, S.L., and Graves, R.E. (1990). Localization of unseen visual stimuli by humans with normal vision. Neuropsychologia *28*, 1231–1237.

11. Raab, D. (1962). Statistical facilitation of simple reaction times. Trans. N. Y. Acad. Sci. *24*, 574–590.

12. Nickerson, R.S. (1973). Intersensory facilitation of reaction time: energy summation or preparation enhancement? Psychol. Rev. *80*, 489–509.

13. Campion, J., Latto, R., and Smith, Y. (1983). Is blindsight an effect of scattered light, spared cortex, and near threshold vision? Behav. Brain Sci. *6*, 426–448.

14. Cowey, A., and Stoerig, P. (1997). Visual detection in monkeys with blindsight. Neuropsychologia *35*, 929–939.

15. Stein, B.E. (1998). Neural mechanisms for synthesizing sensory information and producing adaptive behaviors. Exp. Brain Res. *123*, 124–135.

16. Iacoboni, M., Ptito, A., Weekes, N.Y., and Zaidel, E. (2000). Parallel visuomotor processing in the split brain: cortico-subcortical interactions. Brain *123*, 759–769.

17. Miniussi, C., Girelli, M., and Marzi, C.A. (1998). Neural site of the redundant target effect electrophysiological evidence. J. Cogn. Neurosci. *10*, 216–230.

18. Mordkoff, J.T., Miller, J., and Roch, A.C. (1996). Absence of coactivation in the motor component: evidence from psychophysiological measures of target detection. J. Exp. Psychol. Hum. Percept. Perform. *22*, 25–41.

19. Miller, J., Ulrich, R., and Lamarre, Y. (2001). Locus of redundant-signals effect in bimodal divided attention: a neurophysiological analysis. Percept. Psychophys. *63*, 555–562.

20. Miller, J., Ulrich, R., and Rinkenauer, G. (1999). Effects of stimulus intensity on the lateralized readiness potential. J. Exp. Psychol. *25*, 1454–1471.

21. McMahon, M.J., Lankheet, M.J., Lennie, P., and Williams, D.R. (2000). Fine structure of parvocellular receptive fields in the primate fovea revealed by laser interferometry. J. Neurosci. *20*, 2043–2053.