Visual on- and off-latencies and handedness[1]

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Ten Ss served in this experiment, five right-handed and five left-handed. Every S was tested in a perceived-order situation and by the up-and-down method to determine the relative on-latency for a visual test stimulus, i.e.,

$$\left(\text{ON-Lat}_{\substack{\text{for test stimulus}\\ \text{involving right}\\ \text{hemisphere}}} - \text{ON-Lat}_{\substack{\text{for standard stimulus}\\ \text{involving left}\\ \text{hemisphere}}}\right)$$

and to determine a similarly defined relative off-latency for the same test stimulus. The algebraic difference between the relative on-latency measure and the relative off-latency measure was then found. Data from a previous study had suggested that this "on-off difference" was characteristically positive for left-handed Ss and negative for right-handed Ss. The present data agree. The left-handed Ss were found to differ significantly from the right-handed Ss in the magnitude of the on-off difference. This outcome appears important as a possible clue to functional interhemispheric differences related to handedness.

The present experiment was suggested by results obtained in a parametric study of relative on-latencies and relative off-latencies in visual perception (Kappauf, 1967b). In that study, two small stimuli, a standard and a test stimulus, were presented in a recurring cycle, 2 sec on and 2 sec off. The temporal displacement of one stimulus relative to the other changed from trial to trial. In some series of stimulus presentations, the S directed his attention to the onset of the two stimuli, and on each trial reported which one appeared to come on first. During other series, his task was to observe and report which one went off first. From the record of each series of on-judgments, an estimate was obtained of the temporal separation required between the two stimuli for them to be perceived as simultaneous in onset. This time interval was taken to measure the on-latency for perception of the test stimulus relative to that of the standard. It was recorded as a positive quantity when the test stimulus had to lead the standard in order to appear simultaneous with it, i.e., when the test stimulus had the longer latency. The data for each series of off-judgments were processed similarly to obtain estimates of the off-latencies for the various test stimuli relative to that for the standard. These values, too, were recorded as positive whenever the test stimulus was associated with the longer latency.

Observation was monocular, with the right eye. The standard stimulus, which served as a common reference stimulus throughout the study, was in the right half of the foveal visual field, 15 min from the fixation point. Test stimuli were always to the left of fixation, at a position either 15 min in the left foveal visual field or 2.5 deg in the parafovea. Test stimuli varied in intensity and wavelength from occasion to occasion but "on series" and "off series" involving the same test stimulus were always scheduled as successive tests within the same session. Testing was conducted by the up-and-down method (Kappauf, 1969).

As the data for one of the Ss accumulated through many paired tests with foveal test stimuli, it was noted that the on-latency measures were almost always algebraically larger than their companion off-latency measures. Differences in this direction were, in fact, eventually observed in 28 out of 33 paired foveal tests with this S. For the other two Ss, on the other hand, on-latency measures more often than not were algebraically smaller than their companion off-latencies. Differences in this direction were observed in 19 out of 27 paired tests for one S, and in 19 out of 24 for the other. The probability of each of these tallies deviating this much from a 50-50 split, if relative on-latency and relative off-latency values were really the same, was .0002 for the first S, .052 for the second S, and .007 for the third S (two-tailed p in each case). This left little doubt that the difference in behavior between these particular Ss was a real difference. In view of the fact that the first S was left-handed and the others right-handed, it was conjectured that the result might be associated with handedness and cerebral dominance.

It will be noted that the difference under consideration is not a simple difference between two latencies but, rather, a difference between the differences between paired latencies. It is the difference between the on-latency for the test stimulus relative to that for the standard, on the one hand, and the off-latency for the test stimulus relative to that for the standard, on the other. It may be written:

$$(\text{ON-Lat}_{\text{test}} - \text{ON-Lat}_{\text{standard}}) - (\text{OFF-Lat}_{\text{test}} - \text{OFF-Lat}_{\text{standard}}).$$

For convenience this quantity will be called "the on-off difference."

Under the experimental conditions that have been described, the test stimulus was applied to the temporal part of the right fovea. Related neural events were projected to the right hemisphere, that is, to what has traditionally been considered the dominant hemisphere for the left-handed S and the nondominant hemisphere for the right-handed Ss. The data therefore suggested the following hypothesis, wherein "dom hem" identifies the hemisphere contralateral to the dominant hand, and "nondom hem," the hemisphere ipsilateral with the dominant hand:

$$\left(\text{ON-Lat}_{\substack{\text{dom}\\ \text{hem}}} - \text{ON-Lat}_{\substack{\text{non-}\\ \text{dom}\\ \text{hem}}}\right) - \left(\text{OFF-Lat}_{\substack{\text{dom}\\ \text{hem}}} - \text{OFF-Lat}_{\substack{\text{non-}\\ \text{dom}\\ \text{hem}}}\right) > 0,$$

or

$$\left(\text{ON-Lat}_{\substack{\text{dom}\\ \text{hem}}} - \text{OFF-Lat}_{\substack{\text{dom}\\ \text{hem}}}\right) > \left(\text{ON-Lat}_{\substack{\text{non-}\\ \text{dom}\\ \text{hem}}} - \text{OFF-Lat}_{\substack{\text{non-}\\ \text{dom}\\ \text{hem}}}\right)$$

This is admittedly not a particularly parsimonious hypothesis, but it appeared more acceptable in the light of the result of a brief test in which the left-handed S from the previous experiment made a new set of latency observations using her left eye. Under the hypothesis, the on-off difference should have the same sign regardless of which eye is used. The outcome was as predicted. For the condition where standard and test stimuli both were foveal, white, and at a luminance of .3 mL, the on-off difference for the left eye, based on 60 judgments of stimulus onset and 60 judgments of stimulus termination, was

+30.7 msec. For her right eye, the on-off difference had been +10.2 msec under the same stimulus conditions. Unfortunately, the two right-handed Ss were not available for similar testing.

Because the foregoing observations, limited as they were, lent support to the latency-handedness hypothesis, a search was undertaken for immediately available left-handed Ss who might participate in a more formal test of the hypotheses. This search turned up five. Research time was running short because the lease on the computer and control system that were being used on line in the test situation was about to terminate, but plans were quickly implemented to collect such data as might be possible in the time remaining. The account of this experiment follows.

PROCEDURE

Test Situation

The test situation and general test procedure were in all critical respects the same as those used in that part of the previous study of on- and off-latencies that dealt with foveal test stimuli. The S viewed the two small stimulus spots with his right eye from a distance of 2.18 m. The diameter of each spot was 10 min in visual angle and the two spots were symmetrically placed to the right and left of a small red fixation dot. The total visual angle from the outer edge of the one spot to the outer edge of the other was 40 min. Each stimulus spot was defined by an aperture over a small frosted glass panel that was back-illuminated by "white" light from a glow modulator tube (Sylvania R 1131 C) operated at 30 mA. Spot luminance was .3 mL. The surround and the test room were completely dark. The basic timing cycle for each stimulus was, as before, 2 sec on, 2 sec off.

The S was instructed in the observing task and was given a practice run including trials with very obvious differences in time of stimulus onset. He pressed the right-hand response switch whenever the right-hand stimulus (the standard) appeared first. He pressed the left-hand response switch whenever the left (test) stimulus appeared first. When both S and E were satisfied that the routine had been mastered, the S was given similar practice in observing and judging stimulus termination. A rest period followed this practice.

Data Collection

A single test series to obtain either an on-latency measurement or an off-latency measurement consisted of 60 trials, in five blocks of 12 trials each. Blocks were separated by rest periods of 30 sec. Each block of trials began with a set of four "readaptation" presentations, responses to which were not scored. Each subsequent trial consisted of one or more presentations of the stimulus pair, the S having been advised that the two stimuli scheduled for a given trial would continue to repeat on the 4-sec cycle until he had made a response. Thus, no trials were ever lost due to failure of the S to respond or to respond promptly enough. More importantly, S knew that he was always free to observe as many presentations as he found necessary in order to arrive at a judgment that satisfied him.

Successive trials in each test were programmed from two complementary concurrent up-and-down series (see Kappauf, 1967a). By the end of the fifth block, 30 trials had been given in each series. The step size for three Ss who had had some previous practice at these judgment tasks was 40 to 60 msec. For Ss new to the task, step size was set at 70 or 80 msec initially and was reduced for later series if the consistency of their judgments appeared to warrant it.

The entire testing operation was computer-controlled (Kappauf, 1969). For an on-latency test, the computer controlled the relative time of onset of the two stimuli on each of the trials, and for an off-latency test, the computer controlled the relative time of termination of the two stimuli. At the beginning of each rest period, the computer printed out a summary of the S's data to that point. This summary included the calculated value of the latency of perception of the test stimulus relative to that of the standard, i.e., either ($\text{ON-Lat}_{\text{test}} - \text{ON-Lat}_{\text{standard}}$) or ($\text{OFF-Lat}_{\text{test}} - \text{OFF-Lat}_{\text{standard}}$), depending on the judgment being made.

The plan of the experiment was to obtain four relative latency measurements for each S: two on-latency measures and two off-latency measures, with one test sequence devoted to a pair of measures in the order on-off, and another sequence to tests in the order off-on. Order within the first sequence was on-off for three Ss in each group and off-on for the other two. A pair of measures required about 35 min to complete.

Subjects

There were five right-handed and five left-handed Ss. Handedness inventory data indicated that exceptions to consistent handedness were very rare in both groups.

For five of the Ss, the first pair and the second pair of measures were taken on different days. For two Ss, they were taken on the same day but in different sessions. For two Ss, they were taken within a single session, with a suitable "break" at the midpoint. The 10th S completed only one pair of observations. Illness prevented her from returning for a second session within the time the computer was available.

RESULTS

The data are presented in Table 1. For four of the five left-handed Ss, the on-off difference was positive, as had been predicted. And for four of the five right-handed Ss, the on-off difference was negative, as had been predicted. Under the hypothesis that the probability of correct prediction for each S is .50, the probability of as many as 8 correct predictions in 10 is .055.[4] A test of the hypothesis that the on-off difference is distributed in like manner for right-handed and left-handed persons leads to rejection of that hypothesis: the groups differ significantly (U test, with one-sided alternative: $p = .048$).

The range of values for the on-off difference was very large for each group of Ss. There was reasonably close agreement, however, between the average on-off difference obtained for each of these groups and the average on-off difference found for the same white stimuli with the Ss who served in the previous experiment. These average values are: left-handed Ss in this experiment, +18.3 msec; left-handed S B in previous experiment, +10.2 msec; right-handed Ss in this experiment, −10.0 msec; and right-handed Ss J and P in previous experiment, −12.0 msec.

The present data thus lend support to the hypothesis that right-handed and left-handed persons differ with regard to the on-off difference, and that the sign of the on-off difference is related to handedness. In absolute magnitude, the average on-off difference appears to be of the order of 10 to 20 msec.

DISCUSSION

The present experiment has concerned the separate measurement of relative on-latencies and off-latencies, the comparison of these latencies for the left and right visual fields, and the comparison of the visual performance of left- and right-handed Ss. Related experiments in the literature have individually considered at most two of these problems.

The limited information that is available on the relative magnitude of on-latencies and off-latencies in vision comes primarily from the reaction-time literature. Here one finds four studies that have compared response times to onset with those to termination of a visual stimulus (Holmes, 1923; Jenkins, 1926; Rains, 1961; Woodrow, 1915). Neither visual field nor handedness were variables in any of these studies. Overall, the results are mixed and make it apparent that for centrally viewed

Table 1
On- and Off-Latency Measures and the On-Off Difference for Right-Handed and Left-Handed Subjects
All data are listed in milliseconds. Positive latency measures indicate longer latency for the test (left) stimulus.

Left-Handed Ss	Test Pair	Step Size	Relative On-Latency	Relative Off-Latency	Av. Estim. of σ**	Av. Estim. of $\sigma_{Lat.}$***	Av. Relat. On-Latency	Av. Relat. Off-Latency	On-Off Difference
Wh	1	80	+38.6	−4.2	47	9.5	+28.1	−30.8	+58.9
	2	80/60	+17.6	−57.4	97	17.7			
C	1	80	+27.8	+6.5	21	5.6	+27.5	+5.2	+22.3
	2	80/60	+27.1	+3.8	20	5.0			
Ja	1	80	+6.6	−8.3	61	11.8	+6.6	−8.3	+14.9
Ma	1	80	+6.5	−1.5	23	5.8	+1.7	−1.2	+2.9
	2	60	−3.0	−0.9	22	5.1			
P	1*	70	−8.3	+3.4	22	5.4	−8.8	−1.2	−7.6
	2*	50	−9.2	−5.8	18	4.2			
					Group Averages:		+11.0	−7.3	+18.3
Right-Handed Ss									
M	1	80	+14.6	+6.5	32	7.2	+15.8	+3.8	+12.0
	2	60	+17.1	+1.1	16	4.2			
F	1	40	+0.8	+6.5	18	4.0	+5.4	+8.9	−3.5
	2	40	+9.9	+11.3	20	4.3			
Ju	1	60	−15.3	−10.9	20	4.9	−17.9	−13.3	−4.6
	2	40	−20.6	−15.6	28	5.6			
W	1	50	−0.9	+5.7	23	5.0	−3.9	+4.4	−8.3
	2	40	−6.8	+3.2	18	4.0			
E	1*	80	−60.7	+12.4	50	10.8	−35.0	+10.8	−45.8
	2*	80	−9.4	+9.2	39	8.3			
					Group Averages:		−7.1	+2.9	−10.0

* *Data collected in a single session.*
** *This is the best estimate of the standard deviation of the S's psychometric functions for both the on- and the off-judgments.*
*** *This is the best estimate of the standard error of the individual relative on- and off-latency measures.*

stimulus areas there is no consistently demonstrable difference between reaction time to onset and reaction time to termination.

Latencies for the left and right visual fields have been compared in reaction-time studies and in perceived-order studies, but in this work, Es have regularly used flash stimuli (Efron, 1963a, b, 1-msec flash; Poffenberger, 1912, 4-msec flash; Rains, 1963, 23-msec flash; Rutschmann, 1966, 500-msec flash). Apart from Efron, who specifically studied handedness, only Poffenberger reported on the handedness of his Ss—one left-handed and three right-handed. His data may be collapsed across the variables of stimulated eye and responding hand to obtain an average response time associated with each half of the visual field for each S. These averages fail to indicate that reaction time to flash stimuli in the right and left visual fields is dependent upon handedness, but the experiment cannot be taken as a sensitive one on this point. Considerably more significant are the studies of Efron, studies that resembled the present experiment to the extent that they involved use of the method of perceived order with two test stimuli, one to the left of fixation and one to the right. Efron's situation, however, was specifically designed so that the test stimuli were applied to the two nasal retinae, i.e., the S could see the left visual field stimulus with the left eye only and the right visual field stimulus with the right eye only. Each stimulus spot was removed laterally from the point of fixation by 26 deg and was 17 deg above the level of fixation. The spots were each 3 deg in diam. The S observed repeated presentations of the 1-msec stimuli until he could report if one preceded the other or if they appeared to be simultaneous. The method of limits was employed. Estimates of the point of perceived simultaneity indicated that the 9 right-handed Ss had to have the left stimulus come on significantly earlier than did the 11 left-handed Ss. In other words, the latency of perception of these flashes was relatively shorter for the stimulus that was projected in the hemisphere contralateral to the dominant hand.

In the recent handedness literature, the study by Goodglass and Barton (1963) compared exposure times needed for the recognition of verbal materials presented in the left and right visual fields, of both the left and right eye, and for left-handed and right-handed Ss. The right visual field was found to require shorter exposures for both groups of Ss, a result that it seems proper to ascribe to the confounding effects of left-to-right reading habits (Harcum & Jones, 1962; Heron, 1957). No other effects were significant. It would have required a significant interaction between visual field and handedness to show a dominance-related effect, but its absence means that these data give no support to the hypothesis that visually presented verbal material is more readily perceived when the hemisphere contralateral to the dominant hand is involved.

The newly developed techniques of recording evoked potentials provide a promising physiological approach to the latency problem. It is not yet fully clear what processes are represented in the sequence of waves that comprise the evoked potential, but parametric studies are being undertaken to measure wave latencies and amplitudes as a function of stimulus variables. Increases in stimulus intensity, which are known to decrease visual latency, are reported to decrease latency of the evoked potential and to increase its amplitude (e.g., Clynes, Kohn, & Lifshitz, 1964; Tepas & Armington, 1962). The latency difference that has been observed between the nasal and temporal retinae (e.g., Poffenberger, 1912) is also confirmed in evoked potential recordings (Auerbach, Beller, Henkes, & Goldhaber, 1961; Burns, Heron, & Grafstein, 1960). While most of this work has been done using relatively brief light flashes as the evoking stimuli, on-evoked potentials can be separated from off-evoked potentials by using stimuli of durations that exceed that of the on-potential train. When this is done, two characteristically different potentials are observed (Clynes, Kohn, & Lifshitz, 1964; Efron, 1964). Generality will come only with the accumulation of data for more Ss, but thus far there appear to be no obvious differences in latency for on- and off-potentials. Time to the peak of the major wave, however, appears to be longer for off than for on, and this time value may change with stimulus intensity in a different way for off than for on.

Of special interest for the present discussion is the study by Eason, Groves, White, and Oden (1967), in which evoked potentials recorded over the left and right hemispheres were investigated as a function of stimulation of the left and right halves of the visual field and as a function of the handedness of the Ss. The stimuli in this case were flashes of 10 microsec duration. They were presented binocularly in symmetrically disposed positions 20 deg to the right and left of fixation. For left-handed Ss, stimuli in the left visual field produced potentials in the right lobe that were of significantly greater amplitude than those produced in the left lobe by stimuli in the right visual field. Although a comparable, significant, and opposite effect was not observed for right-handed Ss, the two groups did differ significantly from each other in terms of the ratio of the amplitude of potentials in the right lobe evoked by left-visual-field stimuli to the amplitude of potentials in the left lobe evoked by right-visual-field stimuli.

In view of accumulating evidence to the effect that it is the amplitude of the average evoked potential that is most clearly associated with reaction time (Donchin & Lindsley, 1966; Miller, Moody, & Stebbins, 1969), the findings of Eason et al conceivably warrant a latency interpretation. This would be that the latency of perception of visual flash stimuli is shorter when the dominant hemisphere is involved than when the nondominant hemisphere is involved. Of course, this interpretation has special appeal because it agrees with the results of Efron's latency study cited above.

The Efron and Eason et al studies are of further interest when considered together; both found a significant difference between the measures for right-handed and left-handdd Ss, but in each case the performance of one group was close to that expected under a null condition. In Efron's case, that group was the left-handers, while in the experiment of Eason et al, it was the right-handers. Clearly, the latency effects under study must be small. The fact that they are not easily demonstrable as opposed absolute effects for each handedness group separately, however, need not detract from the merits of the results. Relative effects are the rule in latency studies.

Thus, the combined data of Efron and Eason et al suggest that:

$$\left(\text{Flash Lat}_{\substack{\text{dom}\\\text{hem}}}\right) < \left(\text{Flash Lat}_{\substack{\text{non-}\\\text{dom}\\\text{hem}}}\right),$$

while the hypothesis under consideration in the present paper reads that:

$$\left(\text{ON-Lat}_{\substack{\text{dom}\\\text{hem}}} - \text{OFF-Lat}_{\substack{\text{dom}\\\text{hem}}}\right) > \left(\text{ON-Lat}_{\substack{\text{non-}\\\text{dom}\\\text{hem}}} - \text{OFF-Lat}_{\substack{\text{non-}\\\text{dom}\\\text{hem}}}\right).$$

Exactly how these relations mesh remains for further work to establish. It is interesting to note, however, that Burright (1966) has inferred from intensity functions that latencies to flash stimuli correspond to off-latencies. If this is the case, then the on-off difference may be understood, at least in part, in terms of a hemispheric off-latency difference.

Research has made it increasingly clear that differences in functional organization exist between the two cerebral hemispheres (e.g., Benton, 1962; Cohen, Noblin, & Silverman, 1968), just as anatomical differences exist between them (e.g., Geschwind & Levitsky, 1968; von Bonin, 1962). Two general ideas run through discussions of these functional differences. One is that temporal and phasing factors are important in these differences (see Mountcastle, 1962). The other is that among the dynamic interhemispheric differences there must be some that are specifically related to handedness or cerebral dominance as it concerns handedness. Perhaps an important clue to the latter will be found in the above hypothesis, which expresses a relationship between on- and off-latencies in a manner not heretofore considered.

When new comparative studies of on-latencies and off-latencies in visual perception are undertaken, they should concentrate on tests within the foveal region. The use of foveal locations for studies of interhemispheric differences is not only theoretically reasonable, now that the concept of bilateral cortical representation of the fovea has been discredited (Polyak, 1957), but is also highly practical, because it avoids the problems associated with the increased judgment variability that attends peripheral observations. Of specific interest here is a brief check that the present authors made to ascertain the handedness of the Ss who had served in the Burright (1966) study, where observing conditions closely resembled those used in the present work. Of Burright's three Ss, one could not be reached and one was highly ambidextrous. The third was a consistent right-hander, and so original records were examined to determine what on-off differences had been obtained for her. Relative latency measures, all for her right eye, included 23 paired measures where the test and standard stimuli were located symmetrically in positions 30 min to left and right of fixation. For 16 of these, the on-off differences were negative as expected for right-handed Ss under the hypothesis stated above, and the departure from a 50-50 split was statistically significant (.05 level, one-sided sign test). Other paired tests included five where the test and standard stimuli were located in symmetrical positions 10 deg to left and right of fixation. Here, only one of the five differences proved to be negative. This result is uninformative in view of the small number of observations, but more important is the fact that the variability of the S's judgments was some 50% greater in the 10-deg situation than it was for the foveal situation. Checking out the hypothesis in the periphery, at least by the present methods, will clearly require more extensive testing than in the fovea.

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NOTES

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4. In terms of the character of the binomial distribution for n = 10, rejection of the null hypothesis at the .05 level should follow in eight out of nine times that the above outcome is obtained. See Tocher (1950).

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