Effect of stimulus intensity on manual and saccadic reaction time

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Reaction time (RT) decreases with stimulus intensity. Hughes and Kesley (1984) demonstrated, however, that the effect of stimulus intensity on simple RT is larger for manual than for saccadic responses. We reexamined this relation under various conditions. The dissociation occurred when the task enabled the generation of exogenous saccades. We found, however, no dissociation if endogenous saccades had to be executed. It is hypothesized that the different effects of intensity result from the simplified neuronal processing of exogenous saccades performed in the direct route from the retina to the superior colliculus.

Simple reaction time (RT) gradually decreases with stimulus intensity, reaching an asymptote for extremely intense stimuli. The relation has a very simple mathematical form, called Piéron's law: $RT = RT_0 - kI^{-\beta}$, where RT_0 , k, and β are constants. The applicability of Piéron's law to simple RT has been shown repeatedly (Jaśkowski, 1985; Mansfield, 1973; Pins & Bonnet, 1996; see also Dzhafarov, 1992, for a more sophisticated analysis of this relation). Several studies have made comparisons between the effects of experimental manipulations on simple RT and on visual latency estimated by other methods, such as temporal order judgments (TOJs). Such comparisons have revealed quite different behaviors of simple RT and TOJ. Usually, simple RT underwent larger changes than did TOJ latency. This held not only for stimulus intensity, but also for other variables, such as spatial frequency, attention manipulation, adaptation state, and so forth (for reviews, see Jaśkowski, 1996, 1999). To account for these dissociations, Neumann (1990; Neumann, Ansorge, & Klotz, 1998) proposed a hypothesis that emphasized the difference between judgment and response. He suggested that only a judgment requires that stimuli have to be registered in consciousness, whereas a response can be specified directly by a stimulus, especially when the response is to a large extent automatic. Therefore, as has been suggested by Neumann et al., these two tasks might be mediated by two dif-

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ferent neuronal routes. According to Milner and Goodale's (1995) theory, two visual paths originate from V1. The dorsal path, which projects to the mesial posterior parietal cortex, controls motor guidance-for example, that of aiming movements. It has been thought that conscious perception is not necessary for the guidance of this motor behavior. External stimuli are consciously experienced if they reach the inferior temporal cortex, which is the end station of the ventral path. Many dissociations between perception and action can be interpreted within this theory: Perception and action are mediated by two different and, at least to some extent, independent neural paths. Therefore, in the case also of the dissociation between the effects on simple RT and those on TOJ, it may be assumed that responses can be prepared unconsciously and executed on the basis of information processing in the dorsal path, whereas consciousness, being connected with processing in the ventral path, is necessary for the judgments needed in TOJ.

Although this hypothesis seems to be quite attractive, objections could be raised (Jaśkowski, 1999), since dissociations between the two measures of perceptual latency are not by themselves evidence for the dual-route hypothesis. More specifically, it is not clear why two processing routes should result in different relations between perceptual latency and stimulus intensity. If one were to assume, as many have, that only very early (retinal) stages of processing depend on intensity, no dissociations would be expected. Moreover, the legitimacy of the comparison of the intensity effect on RT versus perceptual latency measured by other psychophysical methods, such as TOJ, is not fully justified principally because of the completely different calculations the neural networks have to accomplish to extract the information needed to perform the tasks (see Miller, Ulrich, & Rinkenauer, 1999).

In this context, a dissociation found by Hughes and Kesley (1984) is of interest. In their study, participants

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made simple reactions to stimuli of different intensities either by pressing a key or by making a saccade to the position at which the stimuli appeared. Although responses, rather than judgments, were required in both these situations, a dissociation occurred: Stimulus intensity had larger effects on manual than on saccadic RTs. According to the logic of the dual-route hypothesis, one would expect no dissociation at all, since both manual and saccadic responses could be directly specified. Thus, this finding might be interpreted as evidence against this hypothesis, but alternatively, there might exist a third route specific to saccadic reactions. Such a possibility could be suggested on the basis of recent anatomical and neurophysiological findings concerning the control of saccadic eye movements. Although all saccades seem to be under voluntary control, exogenous (reflexive) and endogenous (voluntary) saccades are distinguished. The former are triggered by abrupt peripheral events, such as the onset/offset of a light point. The latter are generated in response to symbolic stimuli or instructions (e.g., Walker, Walker, Husain, & Kennard, 2000). It is now also known that in the triggering of these two kinds of saccades, different neural networks are involved. Exogenous saccades are proved to be mediated by pathways from the posterior parietal cortex to the superior colliculus, whereas voluntary ones are mediated by pathways from the frontal eye field to the brain stem (e.g., Gaymard, Ploner, Rivaud, Vermersch, & Pierrot-Deseilligny, 1998).

So one possible explanation of the revealed dissociation is that to prepare a voluntary saccade, the processing of input information needs to be more or less identical to that resulting in the preparation of a manual response. Conversely, triggering an exogenous saccade might rely on simplified processing performed in a third route, in the sense that, in this particular route, not all the visual attributes of the stimulus are recognized. It is, for example, well known that some ganglion cells in the retina project directly to the medio-temporal cortex via the superior colliculus and the pulvinar (Cowey & Stoerig, 1991). This colliculopulvinar route is assumed to be used by blindsight patients (e.g., Milner, 1998), with whom the rudimentary visual ability to "see" stimuli in their hemianopic field is known to be preserved (Weiskrantz, 1997). For example, Weiskrantz, Warrington, Sanders, and Marshall (1974) examined a brain-damaged patient, D.B., who had a visual deficit in the left visual field due to brain lesions in the right occipital lobe. When a light spot was presented in the patient's left visual field, he accurately pointed to the spot with his finger. Patient D.B. also successfully discriminated between horizontal and vertical lines and between pairs of letters, such as "X" and "O," presented for an unlimited length of time. These findings suggest that Patient D.B. could accurately perform some motor responses to a given stimulus even though he was blind to the stimulus. Weiskrantz et al. explained that blindsight may be mediated by the neural pathway from the retina to the posterior parietal cortex via the superior colliculus, bypassing the visual pathway projecting from the lateral geniculate nucleus to the primary visual cortex (where the brain lesions existed). Wurtz and Optican (1994) have claimed that the pathway involving the superior colliculus (the extrageniculate visual system) is primarily concerned with the detection of salient visual events, such as moving objects, rather than with that of stationary ones, and with orientation to visual events in space and saccadic eye movements.

Since in Hughes and Kesley's (1984) study, participants made only simple reactions to peripherally displayed targets (always 10° to the right), reflexive saccades were triggered, and this might be a reason for the dissociation found. Generally, according to the *third-route* hypothesis, one can expect dissociation whenever the target is presented peripherally, and the only information necessary to make a proper saccadic response to the target is its spatial position, not its identity.

The objective of the present study was to replicate and extend Hughes and Kesley's (1984) findings. Besides the simple reaction task, we also used go/no-go and choice tasks in which participants were required to make saccadic or manual reactions according to the current location of the stimulus or according to its meaning (i.e., the stimulus was a centrally presented arrow that pointed to the side to which the reaction was to be made).

GENERAL METHOD

Participants

Eight experienced observers participated in Experiments 1-4. To avoid any learning effects, we randomized the order of the experiments. In Experiment 5, a fresh sample of 9 participants was tested. All the participants were recruited from the student population or the employees at the Institute of Psychology, Kazimierz Wielki University of Bydgoszcz. They were not paid for taking part. All claimed to have normal visual acuity.

Stimuli and Apparatus

The visual stimuli were generated by means of two light-emitting diode (LED) arrays consisting of 64 (8 \times 8) ultra-light-red LEDs positioned 8 mm apart (center to center) and controlled by a microprocessor system. The LEDs were supplied with short current pulses replicated every 9.1 msec. The luminance of the LEDs was controlled by changing both pulse duration and amplitude. With this system, it was possible to change the luminance in the range of 1:10⁴. The stimuli were 400-msec long flashes of several LEDs within the array. Five suprathreshold luminance levels $(-0.8, 0.0, 1.0, 2.0, 2.9 \log$ cd/m²) were used. For peripheral stimulation conditions, two such LED arrays were positioned left and right from a fixation point, with their centers located 10° from fixation. A further single, constantly lit green LED (luminance, 1 cd/m²) was located centrally and served as the fixation point. For central stimulation conditions, only one LED array positioned centrally was used, and two single constantly lit green LEDs were located 10° left and right from fixation, serving as targets for the saccades.

The participants' heads were stabilized by a special head holder that immobilized the back of the head in a constant position. The observation distance was 50 cm.

Eye movements were recorded with an infrared system (Ober 2) with a 200-Hz sampling rate.

Procedure

The experiment was conducted in a completely dark room. One experimental session lasted about a half an hour. Each participant participated twice in such a session. Before each session, the participants were dark adapted for 10 min. Each session was divided into two parts, in which the participants responded with either the hands or the eyes, with this order randomized between participants. Each part, either manual or saccadic, consisted of five blocks of 40 stimuli. During each block, all the stimuli had the same intensity. In blocks with manual responses, the participants were asked to press a keyboard key on the stimulus side (left-ctrl or num-enter). In saccadic intensity blocks, the reaction was a saccade directed to the stimulus position.

The time interval from the participants' response to the next stimulus was sampled from an exponential distribution with a mean of 1,000 msec plus a constant period of 1,000 msec.

Data Analysis

Saccades were analyzed off line. The first saccade, after stimulus presentation, with an amplitude larger than 2° was defined as a saccadic response. Manual and saccadic RTs shorter than 100 msec were regarded as anticipations and were excluded from further analyses. Mean latencies of correct responses were compared in repeated measures analyses of variance (ANOVAs). All *p* values obtained from the ANOVAs were adjusted using the Greenhouse–Geisser coefficient, if necessary.

EXPERIMENTS 1 and 2

In Experiment 1, we attempted to replicate the original study by Hughes and Kesley (1984). As in their study, the subjects performed simple responses either with the eyes or with a hand to a peripherally presented target. Unlike in their experiment, however, the targets could appear either left or right of fixation. However, as in Hughes and Kesley's study, the participants always knew on which side the target would appear. In Experiment 2, a choice-by-location task was investigated-that is, the participants had to press a button on the same side as the stimulus position or had to make a saccade to the stimulus position. In this task, only the location of the stimulus had to be determined, not its identity. Thus, this was also a task in which exogenous saccades were likely to be triggered, and therefore, we expected to find a dissociation similar to that in Hughes and Kesley's original study.

Method

Task. In Experiment 1, each intensity block was divided into two subblocks of 20 stimuli each. In each subblock, the stimuli (four LEDs forming a square) were presented always to one side. Before each subblock, the participants were informed on which side the next 20 stimuli would be presented. In Experiment 2, 40 stimuli were presented randomly either to the left or the right of the fixation point. At the moment of stimulus presentation, the participants had either to make a saccade to the stimulus location (saccadic response) or to press the response keys on the stimulus side while keeping the gaze on the fixation point (manual response).

Results

Mean RTs are shown in Figures 1 and 2, separately for each task. RTs obtained in both experiments were evaluated by using ANOVAs with three within-subjects factors: *task complexity* (simple vs. choice), *response type* (manual vs. saccadic), and *intensity*. Manual RTs were longer than saccadic RTs [267 vs. 392 msec; F(1,8) = 205, p < .0001]. They also decreased with increasing intensity

[F(4,28) = 75, p < .0001]. RTs were independent of task complexity [F(1,7) = 2.89, p = .133]. However, the interaction between task complexity and response type was significant [F(1,7) = 8.4, p = .023]. A post hoc Tukey test showed that for manual responses, choice RTs were longer than simple RTs (374 vs. 409 msec; p = .0098), whereas no difference was found for saccadic RTs (265 vs. 269 msec; p = .94). Of most interest in the present context, the effect of intensity was larger for manual than for saccadic responses [response type \times intensity interaction F(4,28) =5.03, p = .004]. In Figures 1 and 2 (left plots), changes of mean RTs as a function of intensity are displayed-that is, instead of absolute values, we plotted RT for a given intensity minus RT for the maximal intensity. As an inspection of these figures indicates, the significant response type \times intensity interaction means that manual RT increased more steeply than saccadic RT with decreases of intensity. This agrees with what was found by Hughes and Kesley (1984). A separate ANOVA showed a significant interaction of response type and intensity when the intensity range was constrained to the four highest levels [F(3,21) = 4.84, p = .025]. However, unlike Hughes and Kesley's findings, in the present data, saccadic RT increased abruptly for the weakest stimulus, so that the overall increase of RT was equal for saccadic and manual responses. This was supported by an ANOVA performed for only the lowest and highest intensity levels. It showed that the response type \times intensity interaction was nonsignificant [F(1,7) = 0.017].

No other interaction was significant.

Discussion

In Hughes and Kesley's (1984) study, peripheral stimuli were presented to the right of the fixation point, and the participants were asked to respond by pressing a key or making a saccade to the stimulus location. They showed that manual RTs increased more steeply than saccadic RTs when stimulus intensity decreased. Our replication of this experiment was partially successful: Manual RTs increased with decreasing stimulus intensity more quickly than did saccadic RTs, as in Hughes and Kesley's study, for high and moderate intensities. However, for the darkest stimuli, an abrupt increase of saccadic RT occurred. As a consequence, the overall changes of both manual and saccadic RTs due to intensity manipulation were equal.

To account for Hughes and Kesley's (1984) dissociation, we suggested in the introduction a *third-route* hypothesis that assumes that the information necessary to trigger an exogenous saccade is mediated by a route projecting directly from the retina to the superior colliculus. This action was assumed to rely on simplified processing, leading to less of a dependence on intensity than in the case of manual responses. This kind of saccade triggering should not depend on whether participants can predict the location of the next stimulus or not. Thus, we expected a similar dissociation between the effect of intensity on manual and saccadic RTs in Experiment 2, in which the participants had to make a choice on the basis of stimulus

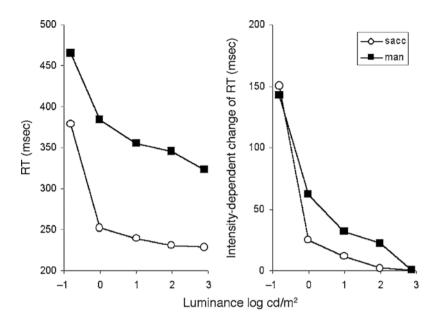


Figure 1. Left: manual and saccadic reaction times (RTs) as a function of stimulus intensity for the simple/peripheral condition (Experiment 1). Right: intensity-dependent variation in saccadic and manual RTs—that is, the difference of RTs for a given intensity minus RTs for the highest intensity. Every point represents the mean across all 8 observers.

location. The results were in accordance with this prediction. To account for the abrupt increase of saccadic RTs for the lowest intensity, one can additionally assume that an exogenous saccade can be triggered only if the stimulus intensity is high enough; when the intensity is too low, a voluntary saccade must be prepared. Although very similar, the experimental conditions used by us and by Hughes and Kesley were not identical. For example, different

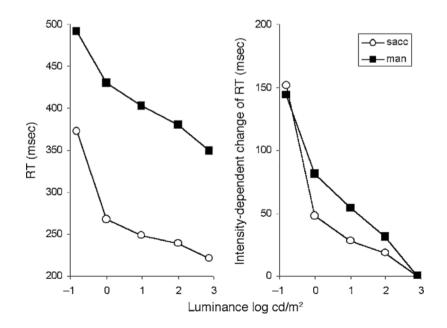


Figure 2. Left: manual and saccadic reaction times (RTs) as a function of stimulus intensity for choice/peripheral condition (Experiment 2). Right: intensity-dependent variation in saccadic and manual RTs. Every point represents the mean for all 8 observers.

adaptation conditions were used in both these studies. Whereas our participants were dark adapted before the session, in Hughes and Kesley's study, the stimuli were displayed against a moderately bright background (0.77 lx). Although the dimmest stimuli they used were only 1.25 times threshold, whereas our dimmest stimuli were substantially brighter than the absolute threshold (about 99%) of the correct responses), it is quite possible that, due to background, their dimmest stimuli were more intense than ours. One can argue in accordance with the above-mentioned suggestion that the lowest intensities used by Hughes and Kesley were still high enough to trigger exogenous saccades. Unfortunately, only the relative intensities of the stimuli used are reported in Hughes and Kesley's study. One can speculate also that in their study, the near-threshold RTs could differentially affect saccadic and manual RTs. Indeed, bearing in mind that the participants awaited a stimulus in every trial, it is conceivable that they occasionally elicited reconnoitering saccades toward the target position when the waiting time seemed to them too long. Such saccades, when delivered 100 msec after the stimulus, were considered to be proper responses in the case of the eye movement task, whereas they were not in the case of the buttonpress task. Although it is not obvious that such artifactual responses necessarily led to a shortening of the saccadic RTs for the dimmest stimuli, an objection could at least be raised as to how reliable the difference between the saccadic and the manual RTs was for that intensity level. Although Hughes and Kesley argued to the contrary, in our meaning such reconnoitering saccades could at least partially account for the lower percentage of misses in the case of saccadic responses.

The different effects of task complexity on saccadic and manual RTs are also of interest. It is very well known that manual choice reactions take more time than do simple reactions. This elongation of choice RTs, known since Donders's time (1868), is assumed to be due to two additional mental operations, choice and discrimination, to be performed by participants. We found such an elongation for manual reactions. No difference, however, was found for saccadic responses: Choice and simple saccadic responses were equally fast. Although inconsistent with Donders' idea, this finding is consistent with the results of some previous studies in which simple and choice saccadic RTs were compared. May, Berg, and Zebley (1999), in comparable conditions, found simple RTs to be only marginally shorter than choice RTs. Saslow (1967) reported no difference between simple and choice RTs even with four alternatives (for a review, see Findley & Walker, 1999). These results could be accounted for within the framework of Findley and Walker's model, which predicts that the effect of spatial selection on saccadic latency should be small. Apparently, the hand sensorimotor system uses quite different mechanism of spatial selection. It should be noted, however, that in a number of studies, the opposite results have been reported-that is, that the number of potential target locations affect saccadic latency (see Dorris & Munoz, 1999, and the references therein).

EXPERIMENTS 3 and 4

In the next two experiments, we compared simple (Experiment 3) and choice (Experiment 4) reactions with stimuli presented centrally. In the simple situation, the participants knew in advance to which place the saccades should be made or with which hand they should respond. In the choice situation, the participants had to choose saccadic direction or response hand according to the identity of the stimulus. According to the third-route hypothesis, we would expect no dissociation of the effects of intensity on saccadic and manual RTs like that found in Experiments 1 and 2, because central stimuli do not trigger exogenous saccades. Thus, the early stages of their processing should be identical with those for the hand motor system. Accordingly, if both systems have these stages in common, we would predict also that in both saccadic and manual systems, choice reactions should take longer than simple reactions, as in the case of manual responses.

Alternatively, one can argue that the dissociation found in Experiments 1 and 2 was not due to different effectors but to the different calculations necessary to execute responses in both tasks (see Ludwig & Gilchrist, 2002). Indeed, in the case of saccadic responses, relatively precise eye movements should be performed. Such precision is certainly not necessary for manual buttonpresses. Although it is not obvious why these differences in the precision of movements can result in different RT-intensity relationships, this hypothesis gives a prediction distinct from that derived from the third-route hypothesis as to the result of Experiments 3 and 4. Since in Experiments 3 and 4 saccadic responses still would need precise eve movements, and manual responses still would need buttonpresses, in assuming this hypothesis, we would expect dissociations similar to those found in Experiments 1 and 2.

Method

Task. As a stimulus, an arrow (formed by six LEDs) pointing to the left or the right was displayed. In Experiment 3, each intensity block was divided into two subblocks of 20 stimuli each. In each subblock, the stimuli pointed always to the one side. Before each subblock, the participants were informed at which side the next 20 stimuli would be presented. In Experiment 4, 40 arrows were presented that pointed randomly to either the left or the right. Two stationary LEDs, which served as saccade targets, were positioned 10° left and right of fixation. Their luminance was constant and equal to 3 cd/m². At the moment of stimulus presentation, the participants had either to make a saccade to the stationary LED pointed to by the arrow or to press the response keys on the stimulus side the arrow pointed to.

Results

Mean RTs are shown in Figures 3 and 4. As before, manual RTs were longer than saccadic RTs [273 vs. 380 msec; F(1,8) = 43.7, p < .0001], and both decreased with intensity [F(4,28) = 51.1, p < .0001]. RTs depended on task complexity [302 vs. 350 msec; F(1,7) = 176.7, p < .0001]. Moreover, the interaction of task complexity and response type was significant [F(1,7) = 14.3, p = .007]. A post hoc Tukey test showed that for both manual and saccadic responses, simple reactions were faster than choice reactions (264 vs. 283 msec, p = .001, for saccadic responses; 341 vs. 418 msec, p = .0003, for manual responses), but for manual responses the difference was much larger.

The effect of intensity was identical for both response types [F(4,28) = 1.18, p = .341] and for both task complexities [F(4,28) = 1.56, p = .220]. The three-way interaction was also nonsignificant [F(4,28) = 0.680 < 1].

Discussion

The dissociation found in Experiments 1 and 2 vanished when the stimuli were presented centrally. This finding corroborates the third-route hypothesis proposed in the introduction, which assumes that the dissociation is due to different intensity processing in the cases of exogenous and endogenous saccades. Since central stimuli do not trigger exogenous saccades, we expected that the impact of intensity on latency should be identical for both manual and saccadic responses. In other words, we assumed that in such a situation, saccadic and manual responses would share the same initial stages of information processing.

The results of Experiments 3 and 4 contradict the alternative explanation of the dissociation found in Experiments 1 and 2—namely, that this dissociation is due to a difference in the complexity of the motor actions to be made in both tasks, rather than to different effectors—because the dissociation disappeared in Experiments 3 and 4, although the complexity of the motor actions in both tasks was identical, as in Experiments 1 and 2.

We predicted also that unlike in Experiments 1 and 2, a difference between simple and choice saccadic reactions would occur. This turned out to be the case. This means that for voluntary saccadic responses, the number of alternative responses plays a role in programming the direction of the saccadic movement. This is additional evidence suggesting that the preparation of a manual response has more in common with preparing an endogenous saccade than with preparing an exogenous saccade. One can, however, wonder why the difference between simple and choice RTs is smaller for saccadic than for manual responses. Indeed, if according to our assumptions, preparation of an endogenous saccade is mediated by the same neural pathway as preparation of manual response, one can expect that the same response selection stage will be used in both cases and, accordingly, the time of selection should be equal. This would be true if the number of alternative responses affects only the selection stage, as is proposed by some RT models with discrete processing stages, such as Sanders's (1980) model. However, Miller and Ulrich (1998) have shown recently that the number of alternative responses affects both stimulus-locked and response-locked lateralized readiness potentials. This suggests that late motor processes also could be influenced by the number of alternatives. These findings suggest that the differences between simple and choice RTs that we found in Experiment 2 for saccadic and manual responses could likely be due to different effects of the number of alternatives on late motor processes, which are obviously different for the two types of response.

EXPERIMENT 5

Experiments 1–4 provide evidence for the hypothesis that input information to the exogenous and endogenous saccades are mediated by two separate neural routes that process

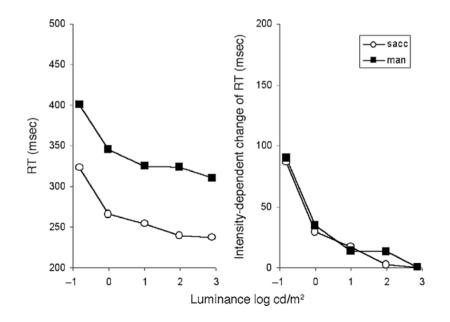


Figure 3. Left: manual and saccadic reaction times (RTs) as a function of stimulus intensity for simple/central condition (Experiment 3). Right: intensity-dependent variation in saccadic and manual RTs. Every point represents the mean for all 8 observers.

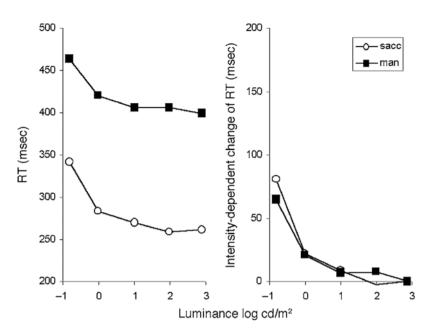


Figure 4. Left: manual and saccadic reaction times (RTs) as a function of stimulus intensity for choice/central condition (Experiment 4). Right: intensity-dependent variation in saccadic and manual RTs. Every point represents the mean for all 8 observers.

stimulus intensity differently. One can, however, argue that peripheral stimulation is responsible for the dissociation. Indeed, we have already shown that the dissociation occurs for peripheral stimuli, and not when stimuli are presented centrally. Thus, one can argue that peripheral stimulation may somehow be particularly favorable for the saccadic system. For example, lower detection thresholds can occur. Therefore, one may expect that with peripheral stimulation, the dissociation will occur even if the position of the next stimulus is unpredictable. No dissociation will, however, be expected for central stimulation. In other words, this suggestion puts the emphasis on the place of stimulation (central vs. peripheral), whereas the thirdroute hypothesis emphasizes whether the saccade is initiated voluntarily or not.

Although peripheral stimulation usually triggers reflexive saccades, the antisaccade paradigm is an example of a situation in which reflexive saccades to the stimulus must be voluntarily suppressed and replaced by a saccade to the opposite side. In such a task, we would expect no dissociation between manual and saccadic RTs. Therefore, to exclude the suggestion that the dissociation is due to peripheral stimulation, we performed Experiment 5, in which while being presented with peripheral stimuli, participants had to generate endogenous, rather than exogenous, saccades. We used, however, a simpler task-namely, go/no-go. Stimuli of different shapes ("x" and "1") were presented peripherally. One of them was defined as the target and the other as the nontarget. The participants were requested to make a saccade to the target and to withdraw their responses when a nontarget was displayed.

Method

Stimuli and Task. As in Experiment 1, the stimuli were generated by means of two LED matrices with their centers positioned 10° from the fixation point. The stimuli had the shape of an "x" or a "+" and were formed by nine LEDs each. The "x" was defined as the target and the "+" as the nontarget. Each intensity block was divided into two subblocks of 40 stimuli each (20 go and 20 no-go trials). In each subblock, the stimuli were presented always to the one side. Before each subblock, the participants were informed at which side the next 40 stimuli would be presented. In the eye movement session, the participants were requested to fixate their gaze on the fixation point and to make a saccade to the target but not to the nontarget shape. In the manual response session, the participants had to press a key on the stimulus side when the target was displayed and to withdraw their response if a nontarget appeared.

Results

Both type of task and stimulus intensity affected RT. As in the previous experiments, an increase of intensity resulted in a shortening of RTs [F(4,32) = 202.5, p < .0001], and saccadic RTs were shorter than manual RTs [427 vs. 512 msec; F(1,8) = 53.5, p < .0001]. The interaction was nonsignificant [F(4,32) = 0.313 < 1].

The results are depicted in Figure 5. Both RT–intensity curves are perfectly parallel, and there are no traces of an *intensity* dissociation.

Discussion

Despite peripheral stimulation, the dissociation disappeared when the task required the generation of an endogenous, rather than an exogenous, saccade. This finding is consistent with our predictions based on the third-route hypothesis.

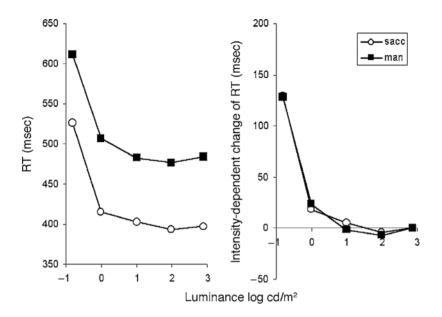


Figure 5. Left: manual and saccadic reaction times (RTs) as a function of stimulus intensity for the go/no-go, peripheral condition (Experiment 5). Right: intensity-dependent variation in saccadic and manual RTs. Every point represents the mean for all 9 observers.

GENERAL DISCUSSION

In this study, manual and saccadic RTs were compared as a function of stimulus intensity. The objective of this study was to shed some light on the dissociation between these two dependent variables found by Hughes and Kesley (1984). More specifically, they performed an experiment in which peripheral stimuli were presented to the right of a fixation point and participants were asked to respond by pressing a key or by making a saccade to the stimulus location. They showed that manual RTs increased more steeply than saccadic RTs when stimulus intensity decreased. We replicated and extended their study. With peripheral stimulation, we partially replicated their findings: For high and moderate stimulus intensities, the RT-intensity curve was steeper for manual than for saccadic RTs. This result was independent of whether the side of stimulus appearance was predictable for the participants, as in Hughes and Kesley's study, or not. Unexpectedly, however, saccadic RTs abruptly increased for near-threshold stimuli, in such a way that the overall changes of both manual and saccadic RTs due to intensity manipulation were equal. If, however, the stimuli were presented centrally, RT-intensity relationships were identical regardless of whether a simple or a choice task had to be performed.

Our results strongly suggest that not all changes of RT due to intensity manipulation may be attributed to the retinal processes (e.g., Mansfield, 1973; Mansfield & Daugman, 1978; Vaughan, Costa, & Gilden, 1966). They rather support the idea, expressed recently by Allik and Kreegipuu (1998), that "it is difficult to maintain the view that there is an invariable VL [visual latency] for the whole visual

system" (p. 137). Similar claims were also made earlier by other authors (Brauner & Lit, 1976; Jaśkowski, 1992; Jaśkowski & Verleger, 2000; Menendez & Lit, 1983; Roufs, 1974; Williams & Lit, 1983). They were formulated usually on the basis of experiments in which simple RT was compared with a visual latency estimated by other methods, such as TOJ. The main result of such comparisons was that simple RT underwent larger changes because of intensity manipulation than did relative latency determined by TOJ. To account for such dissociations, Neumann (1990; Neumann et al., 1998; Neumann & Müsseler, 1990) proposed that once the stimulus-response linkage is defined, conscious control over the response process is not necessary anymore. Such control is, however, necessary if a judgment, rather than a response, is required. Thus, the processing of stimuli in these two situations is performed in two different neural paths. *Intensity* dissociations arise because stimulus intensity is processed differentially in the two paths. Neumann and colleagues did not specify what this differential processing might mean and why the latencyintensity function was flatter for TOJ than for RT.

Comparisons of two such psychophysical methods of latency estimation (RT and TOJ) is, unfortunately, not decisive as to whether intensity processing is constrained to the retina or can affect further stages of information processing, because such a conclusion depends heavily on the model that is presumed to describe how order judgments are performed. For instance, a reasonable assumption is that a judgment of temporal order needs more complete information about events and, thus, a higher criterion than does detection. Sternberg and Knoll (1973) suggested that to maximize the precision of their judgments, participants should rely on the temporal order of the peaks of neural activation evoked by the stimuli, the order of which is to be judged. Conversely, speeded reactions could be initiated whenever the neural activation reaches a given level. Such an assumption has commonly been built into mathematical models of RT (e.g., Grice, Nullmeyer, & Spiker, 1982; Ratcliff & Rouder, 1998). It is rather implausible that these two time markers—that is, the time to cross a criterion and the time to peak—behave identically when a stimulation parameter such as intensity is manipulated (Jaśkowski, 1999).

The present experiments were not, however, concerned with the judgment-response distinction. We have shown that the RT-intensity relationships dissociated depending on whether the participants had to respond by keypressing or by making a saccade, provided that the response was reflexive (exogenous) rather than voluntary (endogenous). In light of recent neuroanatomical findings concerning different neural pathways involved in the generation of exo- and endogenous saccades, we have good reasons to assume that the dissociations arise because intensity is differentially processed in these two pathways. Unfortunately, we can only speculate as to exactly what differential processing means. For example, many models of RT assume that sensory evidence is accumulated before a motor reaction can be delivered (e.g., Grice et al., 1982). The steepness of the accumulation function depends on stimulus intensity, being steeper for stronger stimuli. A lower threshold for response triggering results in a flatter RT-intensity function. With such a model, we can simply assume a lower threshold for exogenous saccades.

Although attractive, the third-route hypothesis proposed in the present article needs further verification, for at least two reasons. First, neuroanatomical data provide information only about which parts of the brain are involved in the processing of different stimulus features, such as intensity, and in the best case, about the overall differences in the processing times for the two neural paths. Little information is provided as to how a feature is processed. Thus, a flatter RT-intensity curve for exogenous saccades could not be derived from the neuroanatomical data. Second, our reasoning relied on the assumption of simplified processing in the third route, in the sense that not all visual attributes are processed in this route. More precisely, in trying to account for our data on the basis of this hypothesis, we have to assume that stimulus shape is not processed in the third route. Unfortunately, the evidence as to what may be processed in the retino-collicular route is unclear. For example, the findings concerning blindsight patients, who are assumed to use this pathway, are still the subject of controversy (e.g., Ptito, Fortin, & Ptito, 2001; Schärli, Harman, & Hogben, 1999). Concerning shape recognition, Weiskrantz et al. (1974) reported originally that the patients were able to discriminate large and simple shapes, such as X or O (see also Sahraie et al., 2003). Their performance was much poorer at discriminating other alphanumeric characters and curvature in the sides of triangles, and they were almost incapable of dis-

criminating rectangles of different ratios of long to short sides when orientation could not be unambiguously used. Perenin and Rossetti (1996) argued that the shape of objects affects blindsight patients' behavior only if they grasp for objects, not if they have to make verbal guesses or match orientation or size with wrist or fingers. More recently, Marcel (1998), using indirect techniques (priming), provided some evidence suggesting that shape is much better perceived by such patients than has previously been thought. Even less is known about whether these patients are able to recognize a given shape by directing their eyes to it, because usually they are asked to perform some manual or verbal tasks. The effect of these patients' practice on their performance is also unclear. Indeed, many blindsight patients have participated many times in different experiments. Indeed, it is known that training can improve these patients' perceptual ability (e.g., Kasten et al., 1999). Finally, one can wonder whether normal participants use the retino-collicular pathway in the same way as blindsight patients.

Conclusions

In five experiments, we explored the dissociation originally described by Hughes and Kesley (1984), which arises when one compares the RT–intensity relationship for manual and saccadic responses. Our results indicate that this dissociation appears only if reflexive saccades, and not voluntary ones, are to be made. This finding, when supplemented by recent neuroanatomical data, strongly suggests that this is due to different intensity processing in the two neural paths involved in the generation of exo- and endogenous saccades. It also suggests that stimulus intensity is processed not only in the retina, but also at some later stages.

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