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Conscious control of movements: increase of temporal precision in voluntarily delayed actions

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Abstract. The variability of simple actions with response to auditory stimuli was studied under different delay conditions. Subjects reacted as fast as possible or with a defined time delay (from 250 to 750 ms) to a tone switching off by pressing a response-key with the left index finger (controlled by the right hemisphere) or with the right one (left hemisphere). For short delays (requested response times below 350 ms) variability of responses was much larger then for longer delays (above 350 ms), especially for the right hand. Thus, precise temporal control on consciously mediated actions sets only in after a rather long delay (in some cases after half a second). Neuronal mechanisms underlying conscious temporal control of actions appear to be different for the two hemispheres.

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Everyday life is characterized by challenges to react sometimes fast to new stimuli and sometimes to delay voluntarily one's actions to such stimuli. The experimental studies have suggested that many aspects of our movements, even when performed intentionally, remain outside our awareness (Castiello and Jeannerod 1991, Libet 1994). Questions could be asked as to what extent subjects can precisely assess their own actions? The empirical evidence has supported the notion that generating a motor reaction to a stimulus and building a perceptual conscious experience of the same stimulus are not controlled by the same mechanisms. For example, Libet and his co-workers (Libet 1985, Libet et al. 1991) reported that intentions to carry out a voluntary action are generated by unconscious cerebral process. A minimum duration of appropriate neuronal activation up to about 500 ms is required in order to elicit a conscious experience or awareness of an event. In agreement with this view, Jeannerod and his co-workers (Castiello and Jeannerod 1991, Castiello et al. 1991) found the relatively constant delay for awareness of visual objects to which a subject was responding by a reaching movement. Verbal responses emitted when the subject become aware of the sudden object jump triggered at the onset of a reaching movement occurred consistently more than 400 ms after the onset of the object displacement. Simultaneously, the temporal dissociation between the motor correction in trajectory of the reaching movement and the verbal response (awareness) was found: the verbal signal was systematically delayed from the motor correction of up about 300 ms, depending on specific conditions. These observations support the hypothesis that the access to awareness is a time-consuming process.

The present experiment was designed to further investigate the different control strategies in the process of movement generation. Since the work of Donders (1969) the reaction time paradigm has been used to better understand central processing, and chronometric analyses of mental processes have been performed using this paradigm. We have become interested in the variability of reaction time and of delayed actions with respect to defined stimuli, and we have come across a new phenomenon on temporal control of delayed actions, which apparently has been until now overlooked in studies using the reaction time paradigm. As the constant finding has been that, under optimal stimulus conditions, reaction time to auditory stimuli is usually shorter and less variable than to visual stimuli, in the present experiment we concentrated on auditory modality.

Seven male and seven female students free of any history of neurological disease volunteered in a study on fast and delayed reaction time. All subjects were right-handed and had normal vision and hearing. The experiment was conducted in a sound proof chamber. The subject sat at a table facing a monitor screen which was placed approximately at a distance of 75 cm. A computer generated pure tone of 600 Hz, comfortably audible, was used as stimulus. The exposure times of the tone were 0.5, 1.5 and 2.5 s, randomly ordered 11 times within each task. The subjects were asked to react as fast as possible or with a specific time delay to the tone offset by pressing a response-button with the index finger. The button was placed on the table directly in front of the subject's left or right hand, at a comfortable distance for pressing. Between the keyboard and the subject there was a platform on which subjects rested their hand while pressing. The responses were given with the left hand (controlled by the right hemisphere) or with the right hand (controlled by the left hemisphere). Each hand was tested separately. There is substantial evidence that the voluntary movements of each hand are controlled by the contralateral hemisphere because of the anatomy of the human nervous system. The differences between hands are accounted by a cerebral dominance mechanism (e.g. Haaland and Harrington 1998).

The requested response times (delays) varied in their duration from 250 ms to 750 ms, in steps of 50 ms. This comprised 12 tasks; the one with the fastest reaction and the remaining 11 with various delays were employed in separate sessions. In each session only one delay time and one hand was tested. Both the requested response time (the target reaction time) and the reaction time achieved by the subjects in a given trial were displayed on the screen and recorded with the accuracy of $\pm$ 0.5 ms by the especially designed computer programme. A buzzing sound from the computer signalled both the beginning and the end of each task. Moreover, the subjects were asked to avoid any mental counting during their delayed response.

Each trial began with the indication of the required target reaction time by a number on the screen, followed by the tone presentation. After the subject's response, the reaction time achieved was displayed on the screen. At the beginning of each session the subject was taught to perform the requested task (15 practice trials), followed by the experiment proper (33 test trials). The inter-trial intervals were 2 s. The experiment consisted of 24 sessions (12 various tasks x 2 hands) lasting approximately 10 min each, separated by 2 min rest-breaks. The sessions were randomly ordered to avoid any order effects.

The standard deviation (SD) of mean reaction time achieved (RT) was used to measure response precision. As an increase of mean RT (requested targets were from 250 ms to 750 ms) is usually accompanied by an increase in SD, to compare the response precision in the employed sessions, a transformation of SD was used. The transformation was defined as a/b (where a = SD found for the requested response time in the given subject and b = the group mean RT for this response time divided by the group mean fastest RT). The SD values derived from the fastest reaction remained untransformed. Such a transformation allows to measure regularity of subjects' responses relative to overall rate, i.e. as a proportional quantity, rather than as an absolute measure. It takes into account typical individual differences in the fastest reaction time, which could strongly influence the performance, especially of shorter delays depending on the shorter or longer fastest reaction. Moreover, a simple change of speed, i.e. the time scale disturbance (target over/underestimation) will slightly modify the transformed standard deviation (t_{SD}), but will strongly modify, for example, the coefficient of variation.

In Figure 1 an example of the performance of one subject using his left hand is given. As can be seen, variability of responses rises sharply for the first delay (250 ms) and remains at this level up to 350 ms. For longer delays (starting with 400 ms) variability decreases and remains at low values up to the longest delay employed here (750 ms). It is important to note that response variability shows a three-fold increase between the fastest reaction and response delays between 250 and 350 ms followed by a two-fold decrease for longer delays.

Statistical analysis for all data was performed by means of 3-factor analysis of variance, ANOVA, applied to the t_{SD}. For the t_{SD}, the analysis with gender (male/female) as a between-subjects variable, delay (12 tasks) and hand (left/right) as within-subjects variables indicated a highly significant delay effect ($P<0.000$, $F_{11,132}=10.434$), modified by the significance of the interaction: hand x delay ($P<0.04$, $F_{1,12}=5.074$).

As can be seen in Fig. 2, the precision level varied between the left and right hand, depending on the required target. Although for each hand, performance was highly variable for short delays as compared to the fastest RT (approx. 200 ms, on average), this relationship was stronger for the right than for the left hand (see Fig. 2).

These results indicate that conscious control of movements with respect to their temporal variability sets in after a rather long delay, much longer than the usual simple RTs (Libet 1985, Libet et al. 1991, Libet 1993). Furthermore, other than suspected (e.g., Efron 1990, Nicholls 1995) there seems to be an advantage of left hand control, i.e. a temporal superiority of right-hemisphere functions.

These results appear to have some interesting implications. At first sight the results may appear as con-

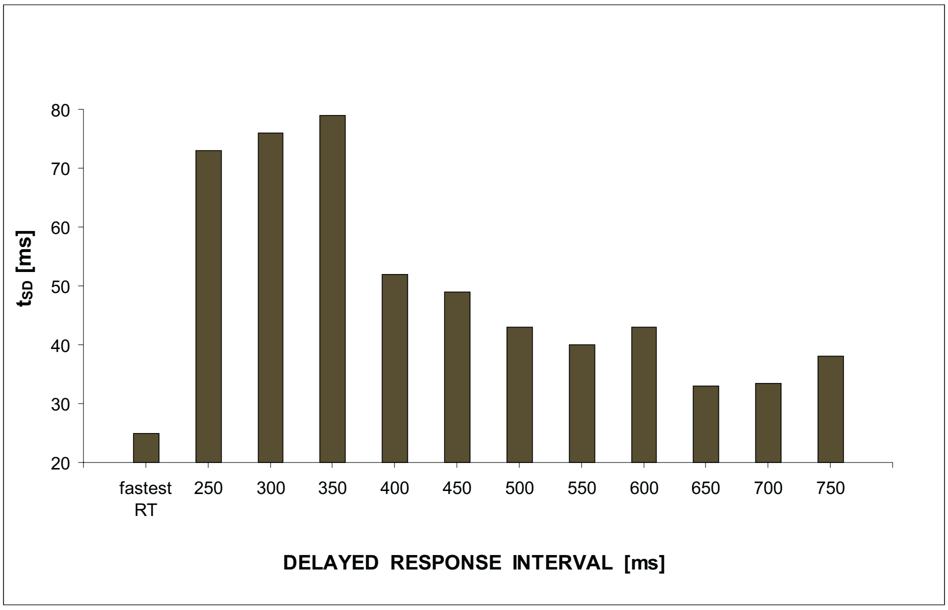

Fig. 1. An example of the left hand performance in one subject.

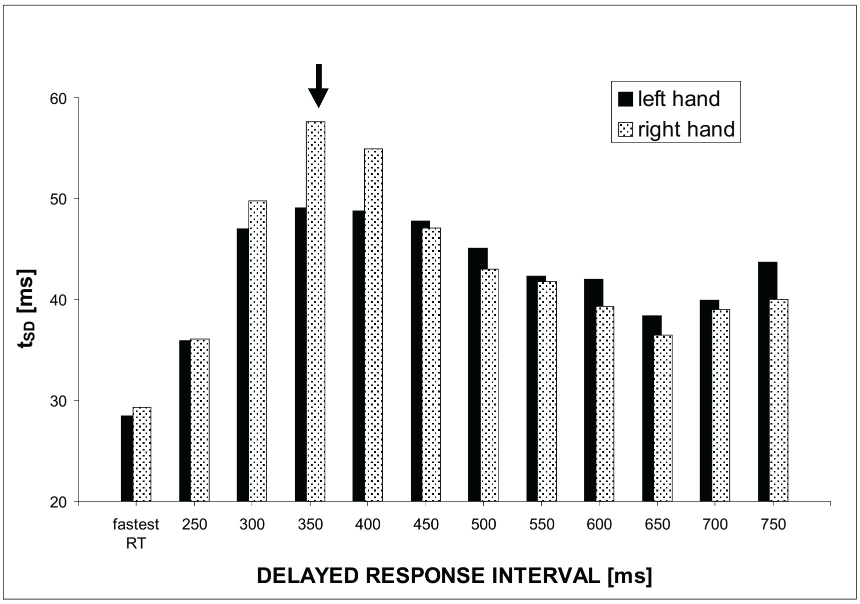

Fig. 2. t_{SD}s for the left and right hand as a function of various tasks. The following differences were proven to be significant: left hand: fastest RT vs. 300 ms $P<0.03$, 250 vs. 350 ms $P<0.02$; right hand, fastest RT vs. 300 ms $P<0.005$, 250 vs. 300 ms $P<0.03$, 250 vs. 350 ms $P<0.005$, 350 vs. 450 ms $P<0.01$, 400 vs. 450 ms $P<0.05$, 400 vs. 500 ms $P<0.05$; left vs. right hand: 350 ms $P<0.01$ (indicated by an arrow).

tra-intuitive because one might expect that the variance in reacting to stimuli increases linearly with longer response times. The systematic reduction for longer response times suggests that for the execution of responses two qualitatively different neuronal (i.e. data-generating) mechanisms are responsible (Libet 1985, Castiello and Jeannerod 1991, Libet et al. 1991, Fourneret and Jeannerod 1998), i.e., one for shorter and the other for longer intervals. Alternatively, it can be assumed that after a delay time of approximately 400 ms an additional mechanism sets in, and on the basis of other evidence this contributing mechanism might be linked to attentional control. Furthermore, it can be concluded that conscious control contributes to a reduction of temporal variance, which is contrary to the common belief that automatic movements, which are ballistically programmed (i.e., inertial movements triggered without any active feedback control and ability to correct the direction of a tracking movement), show less variability. As conscious control is presumably related to cortical mechanisms, it can be concluded that temporal precision is augmented by the cortical machinery, and that contrary to common belief the right hemisphere is superior to the left hemisphere. As the right hemisphere plays a major role in attentional control (Posner 1995), the results suggest that right hemisphere attentional functions are responsible for the precise time control of voluntarily controlled actions.

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