FOURNERET, P., PAILLARD, J., LAMARRE, Y., COLE, J. and JEANNEROD, M.
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Neuroreport. 2002 Mar 25, 13 (4). 541-547

Original manuscript

Lack of conscious recognition of one's own actions in a haptically deafferented patient

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Abstract

How do we become aware of our own actions ? This classical question is still a matter of debate : does consciousness depend on central efferent signals or derive from peripheral information ? In this paper, we had the opportunity to study a haptically deafferented patient using a well-tested experimental paradigm where a cognitive conflict is produced between motor intention, proprioception and visual feedback. Our results show that the patient was able to solve the conflict and to generate accurate movements to a target in the absence of proprioceptive feedback and with very limited visual feedback from her movements. Yet, she could not report any conscious perception of the conflict and showed no conscious knowledge of her actual performance. We suggest that information derived from efferent processes cannot in themselves be a source for conscious experience about our own actions.

Key words : awareness of action ; deafferented patient ; visuo-motor conflict

INTRODUCTION

To make a conscious judgement about one's own motor performance, several sources of information can be used. Visual cues, directly derived from vision of the moving segment, or indirectly from the effects of the movement on external objects, provide a major contribution for monitoring one's actions. Another critical source is haptic perception, derived from movement-related mechanical deformations of the limb, through receptors located in the skin, joints and muscles. Position sense, the sense of the position of the limb at the end of a movement, is one of the conscious counterparts of these proprioceptive reafferences produced by the movement.

Another classically considered source of information about one's own movements relates, not to sensory signals, but to the central mechanisms originating in the motor system during the production of a movement. It has been held that the motor commands sent to the spinal motoneurons might be shared by other areas of the nervous system, where a representation of the forthcoming movement would be stored [1,3]. There is a longstanding controversy about the respective roles of these central discharges and of the sensory reafferences in conscious knowledge about actions. In the classical "William's debate", William James defended the opinion that all that we know about our movements is based *a posteriori* on information from sensory organs, whereas Wilhelm Wundt, on the contrary, held that our knowledge is based *a priori* on efferent information of a central origin (for a detailed account, see ref. 4).

The ability to recognize a movement as one's own requires that the effectively produced motor pattern can be compared with the content of the corresponding intention. Does this process imply the availability of haptic cues ? Or, conversely, can motor commands in themselves be sufficient ? The main problem here is a methodological one, mainly because of the difficulty to suppress haptic sensations in conscious humans : one of the most popular methods, ischemic block of one arm has been questioned because it affects, not only sensory, but also motor fibers [5]. Curarization of one limb, which excludes muscular contractions (and the correlative sensory input) from that limb, is another possibility : if subjects report sensations from their attempts to move their paralyzed limb, these sensations should arise from their motor commands, not from proprioceptive input. The available evidence shows that no perception of movement arises in this condition [6]. However, experiments with partial curarization of the arm suggest a more balanced conclusion : subjects requested to estimate the heaviness of weights that they attempted to lift with their weakened arm report an increased perceived heaviness. This illusion was interpreted as reflecting the consecutive increase in motor outflow needed to lift the weights [7]. This result provides an indirect evidence as to the possibility for central signals to influence conscious experience.

A more direct solution to this problem would be to examine patients with complete haptic deafferentation of pathological origin (e.g., by sensory neuropathy). However, the rare patients with such a pathology have mostly been tested for their ability to control their movements in the absence of proprioceptive input (in terms of accuracy, kinematics, or coordination, for example), not for their ability to recognize movements they had performed [8]. In the present study, we have taken advantage of the condition of GL, a well documented haptically deafferented patient. Because GL has no haptic information about the movements she performs, and visual feedback from the same movements can be either systematically distorted or suppressed, the only information on which she can rely to form a phenomenal experience about her own movements should be derived from the motor commands she generates for producing these movements. Thus, an experimental study of action recognition in this patient represented a unique opportunity to answer the open questions about the contribution of central signals to the conscious knowledge about our behavior and our own body.

MATERIALS AND METHODS

Subjects : A deafferented patient, GL, aged 52 years, and five healthy control subjects (mean age 42.6 years) participated in the study. The experiments were performed in compliance with the relevant French legislation about human participation on experimentation. All subjects gave their consent to take part in this study.

Subjects were right handed according to the Edinburg Inventory [9] and naive to the purpose of the experiment. G.L presented a permanent and specific loss of the large sensory myelinated fibers (testified by a biopsy at the level of the sural nerve) from her whole body below the nose level, following two episodes of sensory polyneuropathy. This illness resulted in absence of tendon reflexes in the four limbs as well as a total loss of the senses of touch, vibration, pressure and kinaesthesia in neck, trunck and limbs. Thus and despite normal motor nerve conduction velocities explored by electromyogrphy [10], GL had no sensation or control of her head/neck and limb position or movement with her eyes closed. Confined to a wheelchair, she does most of the daily manual activities under constant visual control (for a full clinical description, see below and ref.11). This clinical picture has been regarded as stable for the last twenty years.

Apparatus: The experimental device consisted of a 12'' x 18'' graphic tablet [Numonics – GridMaster D45 ; Resolution, 0.025 mm ; Accuracy : +/- 0.01'' ; Output Rate : up to 200 points/second] placed on a regular table, and connected to a computer. The computer screen was placed horizontally at 62 cm above the graphic tablet. A circular mirror (35 cm in diameter) was placed horizontally halfway between the screen and the tablet. The subjects sat on a chair facing the table. They looked at the mirror and held in their right hand a stylus connected to the graphic tablet. Their right hand was placed on the tablet, below the mirror, and was thus invisible to them. When tracing a line on the tablet, the subjects could see through the mirror a red line appearing on the computer screen in exact coincidence with the displacements of the tip of the stylus on the tablet. The output of the graphic tablet was processed by the computer using a simple algorithm for adding a linear directional bias. When the bias was set to the right, e.g at 15°, a line traced in the sagittal direction on the tablet appeared to the subject to deviate to the right at an identical angle [12].

Procedure: At the beginning of each trial, the subjects placed the stylus tip on the starting point located on the tablet close to the body midline (a green point, 3x4 mm). They were instructed to reach a yellow target (3x4 mm) located on their sagittal body axis at 22 cm from the starting point. They had to draw a continuous line as straight as possible, keeping the hand in contact with the graphic tablet. After the trial had been completed, the screen was blanked and a new trial started when the subjects placed the stylus on the starting position. Considering the difficulty of GL to hold the stylus in the absence of vision of her hand, the stylus had to be replaced by a mouse. The mouse was held in the palm of her right hand with adhesive tape. The extremity of her major finger corresponded to the contact point with the digitizer tablet. Finally, the duration of each trial was fixed to 7 sec. After a training session with no bias, participants were subjected to two experimental sessions :

1. In Session I, twenty trials biased to the right were performed. The amplitude of the bias went from 1° to 20°, increasing by 1° at each new trial. The instruction given to the subjects was to trace a line as straight as possible so as to reach the visual target. In order to do so, the subjects had to compensate the visuomotor discordance and thus to trace a line with a deviation to the left roughly equal to the angular bias. At the end of each trial, the subjects were asked whether the line they had traced was the same as the line they had seen in the mirror. The angle of the bias at which they became aware of the conflict (i.e., when they first answered no) was noted. Subjects were then asked to give a verbal estimate of their motor performance. They were shown a card with lines drawn at different angles from a starting point. These lines were numbered from 1 to 31. Lines 1-15 deviated to the left with respect to the axis of the card, lines 17-31 to the right. The line numbered 16 was aligned with the card axis. The question to the subjects was : "According to your own impression, which line corresponds to the actual trajectory drawn by your hand ?". The verbal response had to be given by reading the corresponding number on the card.
2. In Session II, twenty trials biased by 15° to the right, were performed. In this condition, the visual feedback from the movement was partially blocked throughout the testing, by using a mask obscuring the first two thirds of the trajectory, so that the subjects were able to see the path of their hand only near the end of the trial. The instruction given to the subjects was identical to the first session, namely to trace a line as straight as possible, such that when coming out of the mask, it would be as close as possible from the target position. To fulfil the instruction, subjects had to become aware of the visuomotor discordance and then to intentionally select below the mask a hand path deviating to the left (i.e., opposite to the bias) by the same angle (15°) with respect to the sagittal direction. At the end of this session, subjects were asked to verbally report their impressions and, specifically, the manual strategy they had adopted to carry out the task.

Data analysis: In the two sessions, sensory-motor adjustment to the bias was evaluated by computing the square of the Root Mean Squared Error or a^2:

$$\boxed{a^2 = \frac{1}{x_f - x_i}\int_{x_i}^{x_f}(f_s - f_r)^2\,dx}$$

where

x_i is the initial position of the stylus tip,

x_f the final position of the stylus tip,

f_s the real trajectory realized by the subject and

f_r the ideal trajectory to correct the deviation.

This ratio corresponds to the average deviation of the trajectory made by the subject from the theoretical line that would perfectly compensate for the bias [13]. In other terms, the more the score of this ratio approaches 0, the more the trajectory can be considered as parallel to the line between starting point and target. This measure has moreover the advantage of avoiding cancellation between right and left side deviations from the ideal line.

Finally, movement duration was measured for each trial. In this experiment, duration was measured only for the first 80% of the distance to the target, due to the large variability of the final part of the trajectory.

In session I, the threshold of conscious perception of the bias (the angle at which the subjects explicitly reported a feeling of discordance between what they did and what they saw) and consecutively the verbal responses for each subject were recorded and analyzed. In session II, the number of trials necessary to trace a trajectory with a^2 lower or equal to .01 as well as the number of correct trials carried out thereafter were recorded for each subject. Awareness of the conflict was appreciated by the explicit report of a correction to the left.Because of variance heterogeneity (*Levene's test* ; $p< .008$), data obtained from controls and deafferented subject were submitted to non-parametric tests. *Spearman rank order* *correlation test* was used to study the relation between the independent factor (Angles or Trials) and the dependent factor (a^2) for the patient and controls. *Mann-Whitney U test* was used to compare GL's performance to that of control subjects.

RESULTS

In Session I, an angular bias to the right, increasing from 1° to 20° over successive trials, was introduced. This required from the subjects that they drew on the tablet a line increasingly rotated to the left, to compensate for the bias. Subjects, including patient GL, performed the task without difficulty and were able to compensate for the bias. As Figure 1 shows, the performance of the control group tended to deteriorate and to become more variable while the bias increased. In patient GL, the performance remained relatively stable and did not seem to be affected by the increasing bias. Even if the movement duration of G.L's trials was shorter [median = 1.11 sec] than controls [median = 2.59 sec] (see the insert in Fig. 1), we did not find a significant correlation between this variable and the angular bias, contrary to the control group for which the movement duration increased with the disturbance progression [$R = 0.31$; $p < .001$].

During the session, GL never explicitly reported a feeling of discordance between what she had seen and the movements she thought she had made. Conversely, all the control subjects became aware of the visuo-motor conflict at an average angle of bias of 6 degrees (median value). This result was obtained by asking the subjects, at the end of each trial, to estimate verbally, by reading a value on the card, the angle by which they thought their hand had deviated in either direction for producing the line. Figure 2 shows the median values of the verbal responses for the normal subjects and the patient. The pattern of their responses differed significantly [$U = 469$; $z = 3.70$; $p < .0002$]. While GL answered values around 16 (mean = 16.50 +/- 1.10) whatever the angle of trials, indicating that she thought she had drawn the line in the sagittal direction, the responses of the control subjects significantly correlated with the angle of the disturbance [$R = - 0.31$; $p < .001$]. Hence, control subjects were clearly aware - although by underestimating it - of a displacement of their hand towards the left to compensate for the bias.

In Session II, the mask placed on the screen occluded the first 2/3d of the trajectory. A constant bias of 15° to the right was introduced for all 20 trials. Thus, in order to compensate for this bias, the subjects had, first, to discover the amplitude of the bias when they first saw the line coming out of the mask, and, in subsequent trials, to use a strategy of compensation beginning during the phase of the movement occluded by the mask (see

Fig. 4 for illustrative trials). As shown by changes in parameter a^2 in Figure 3, the effectiveness of the compensation for the bias significantly improved in the control group (i.e., the value of a^2 decreased) from the first to the 10th trial [Friedman's ANOVA by ranks : Chi ^{2} = 33.08 ; $p < .0001$]. After the 11th trial, adaptation tended to remain stationary [Friedman's ANOVA by ranks : Chi ^{2} = 6.07 ; $p < .73$]. GL's performance significantly differed from that of the control group [R= -0.69 ; $p < .000001$], as no significant correlation between the values of the dependant factor (a^2) and the trials was observed [R= -0.12 ; $p < .61$]. A closer look shows that GL was able to produce movements with only little error ($a^2 = 0.0059$) already from the third trial. Unlike the control subjects, however, she could not durably maintain her performance, and produced trials with large errors intermingled with good trials. GL's movements duration was slightly shorter (median = 1.91 sec) than in controls (median = 2.26 sec) even if this difference was not significant (Fig 3, insert).

Inspection of the trajectories made by control subjects and by GL reveals a further interesting difference in the pattern of corrections in control subjects and in GL. Whereas in normal subjects corrections always appeared after the line became visible (i.e., they used the distance between the actual visual position of the line and the position of the target as a cue), GL's corrections were often generated while the line was still hidden by the mask ; Yet, these corrections were consistently in the target direction. This striking phenomenon happened in 16/20 trials. In addition, GL could also produce visual corrections when necessary, after the line became visible. Figure 4 compares trajectories of the same rank in the sequence of trials in GL and in an average control subject. The difference in location of the correction is clearly visible.

In spite of expressing perplexity at the end of some trials, G.L never became aware of the bias and, consequently, of any strategy of correction she had to apply to correct for it (this was also the case in an post-hoc control session in which the bias went until 40°). However, it is worth noting that she explicitly mentioned the 'difficulty' to reach the visual target and, sometimes, the 'effort' of concentration that this required from her. Conversely, during the session debriefing, all control subjects reported that they had to impose a leftward direction to their hand movements in order to achieve the task. Three of them explicitly blamed the experimental paradigm to explain the discordance they had felt. The other two attributed their errors to bad performance from their part.

DISCUSSION

One should first consider GL's strategy in performing actions toward a visual goal in an experimental situation requiring adaptation to a perturbation. In the first series of trials (Session I) GL was able to build a strategy for directing her hand away from the target position, in order to bring the visible line in the straight ahead direction. The most likely hypothesis for explaining this behavior is that she relied on the visual difference between the direction of the visible line and the location of the target for redefining the direction of her movement at each new trial. As a consequence, as Figure 1 shows, she maintained the same level of mediocre performance over the 20 trials. This strategy was very different from that of control subjects who were likely to use the typical visuomotor adaptation mechanism described in other similar situations, like prism adaptation [14]. They performed accurately throughout, except for an increase in variability for the trials with the largest bias. The increase in movement duration over succesive trials, observed in control subjects and not in GL, is an additional argument in favor of this strategic difference.

In Session II, GL was also found to be able to compensate for a fixed perturbation imposed to her movements, in the absence of any direct sensory information. She succeeded within a few trials in modifying the well-established correspondence between target position and the diection of her movements. This modification was not an effect of progressive learning : it was a brisk recalibation of movement parameters according to the new visuomotor rule. Indeed, her performance at the third trial was already at the level reached by the control group at the 8th trial only (Fig.3). In fact, GL appeared to encode the required movement direction from the onset of the trajectory, and to perform the movement in a completely open-loop fashion. This strategy was reflected in her everyday behavior. For grasping an object placed at a distance, GL tended to throw her hand in the direction of that object with great accuracy : in other words, her movements were based on computation of visual localization of the target and feedforward control of the movement. Vision was not used for online guidance, but only for calibrating motor output (for a full description of this behavior, see ref. 15). The existence of corrections below the mask, i.e. in the absence of any error feedback, is not incompatible with the notion of open-loop programming. Purely feedforward mechanisms have been postulated to be able to detect errors with respect to a simulated trajectory and to update the trajectory of the ongoing movement [16].

The second point to be discussed is the striking finding that GL, in spite of achieving the visuomotor task rather correctly, was unaware of having to compensate for a bias introduced by the experimenter between the seen position of the target and the actual trajectory of her hand. This bias required to deviate the hand movement by up to 20° away from the apparent position of the target in order to reach for it. Control subjects, in Session I, became aware of the existence of a bias when it exceeded 6° on average and realized that they had to shift from an automatic to a conscious strategy for achieving the task (in confirmation of previous results [17]). In Session II, they were systematically aware that they had to learn to compensate for a large bias. Patient GL, in the absence of proprioceptive cues from her movements (and, in Session II, with strongly reduced the visual cues), could not report how she got to the target. The only sensations she reported were vague feelings of effort and difficulty of the task. Does this result mean that the role of central cues should be limited to such a secondary role and should not be the source of more accurate sensations ? Although this interpretation may be correct, it does not account for the complete set of events arising during the voluntary execution of a movement. The most recent models of action monitoring postulate that central discharges corollary to the motor commands are used as references for a desired action, against which reafferent sensory signals from the executed movement can be compared [18]. Although in GL, the corollary discharges representing the desired movement were generated along with the motor commands (as already postulated for explaining the corrections), the comparison mechanism could not take place because no reafference from the executed movement was present. This reasoning would imply that this conscious information about the movement would be derived, not from the corollary signals themselves, but from the output of the comparison process [19].

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Acknowledgements : This research was supported by the Programme Cognitique from the French Ministry of Education. Experiments were conducted with the active collaboration of the subject G.L. We sincerely thank her for her cooperation. Technical support of Lionel Granjon is gratefully acknowledge. P. Fourneret was supported by a fellowship awarded jointly by the CNRS and the Hospices Civils de Lyon.

Figure captions

Fig. 1. Visuomotor performance of patient GL (left) and control subjects (right) as a function of the increasing bias from 1° to 20° (ordinates: Angle in degrees). Performance is expressed with parameter a^2 which reflects the difference between the line actually drawn by the subject and the ideal sagittal line (see Methods). Only the trajectories for which the subject had covered more than 90% of the distance separating the starting point from the target were kept for analysis. Control subjects covered significantly less distance than the patient [U = 198 ; z = 5.62 ; P < .00001]. In both GL and control subjects there was no significant correlation between the distance covered and the angles (Spearman rank order correlation test).

Insert : measures of movement duration showing that G.L movements were shorter than those of control subjects [U = 106 ; z = - 6.28 ; P < .00001].

Fig. 2. Conscious monitoring of the movements performed in Session I by patient GL (left) and control subjects (right). The results are expressed in terms of subjects' verbal responses (reading of the angle on a chart, see Methods), as a function of the angle of bias. If subjects read the actual value of the angle, their responses would fit the line indicates by crosses. Note that control subjects tend to follow this line with a gain of approximately 0.5.

Fig. 3. Visuomotor performance of patient GL (left) and control subjects (right) during attempt to compensate for a 15° constant bias, in the absence of visual reafferences during the first 1/3d of the trajectory, as expressed by parameter $a2$ as a function of the rank of trials. Note quick adaptations in GL as compared to progressive learning in control subjects. Only the trajectories for which the subjects had covered more than 70% of the distance separating the two targets were retained for analysis. Control subjects covered significant less distance that the patient [U = 310 ; z = 4.85 ; p < .00001]. No significant correlation between the distance covered and the angles was observed in both control subjects and the patient (Spearman rank order correlation test). The control subjects globally produced more trajectories to the target than the patient [U = 143 ; z = 3.19 ; p < .001].

Insert : movement duration. G.L 's trials were shorter (median = 1.91 sec) than controls (median = 2.26 sec). Non significant difference

Fig. 4. Selected samples of trajectories from Session II in patient GL (left) and in a control subject (right). In both subjects, a trajectory of the same rank in the sequence of trials has been selected (trial n° 6). The red line corresponds to what subjects see in the last section of the trajectory (after getting out of the opaque mask); the black line corresponds to what subjects actually do in order to get to the target; the dotted line on GL's trial indicates the amplitude and direction of the bias (15°). Note that, in the control subject, the trajectory was corrected only when the line became visible. In contrast, GL, in this particular trial, produced two types of correction : several "open loop" corrections below the mask and one final, visual, correction.

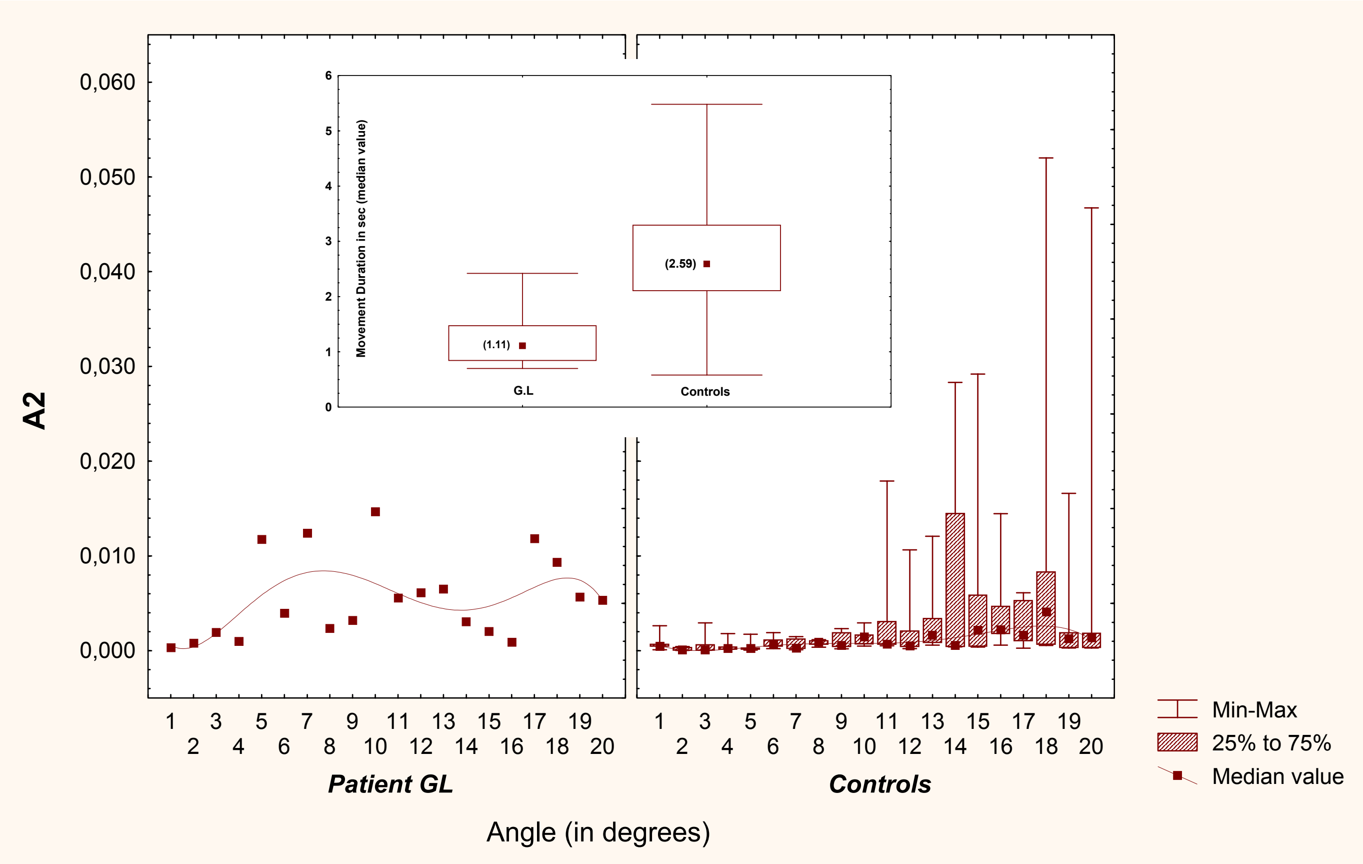

Fig. 1

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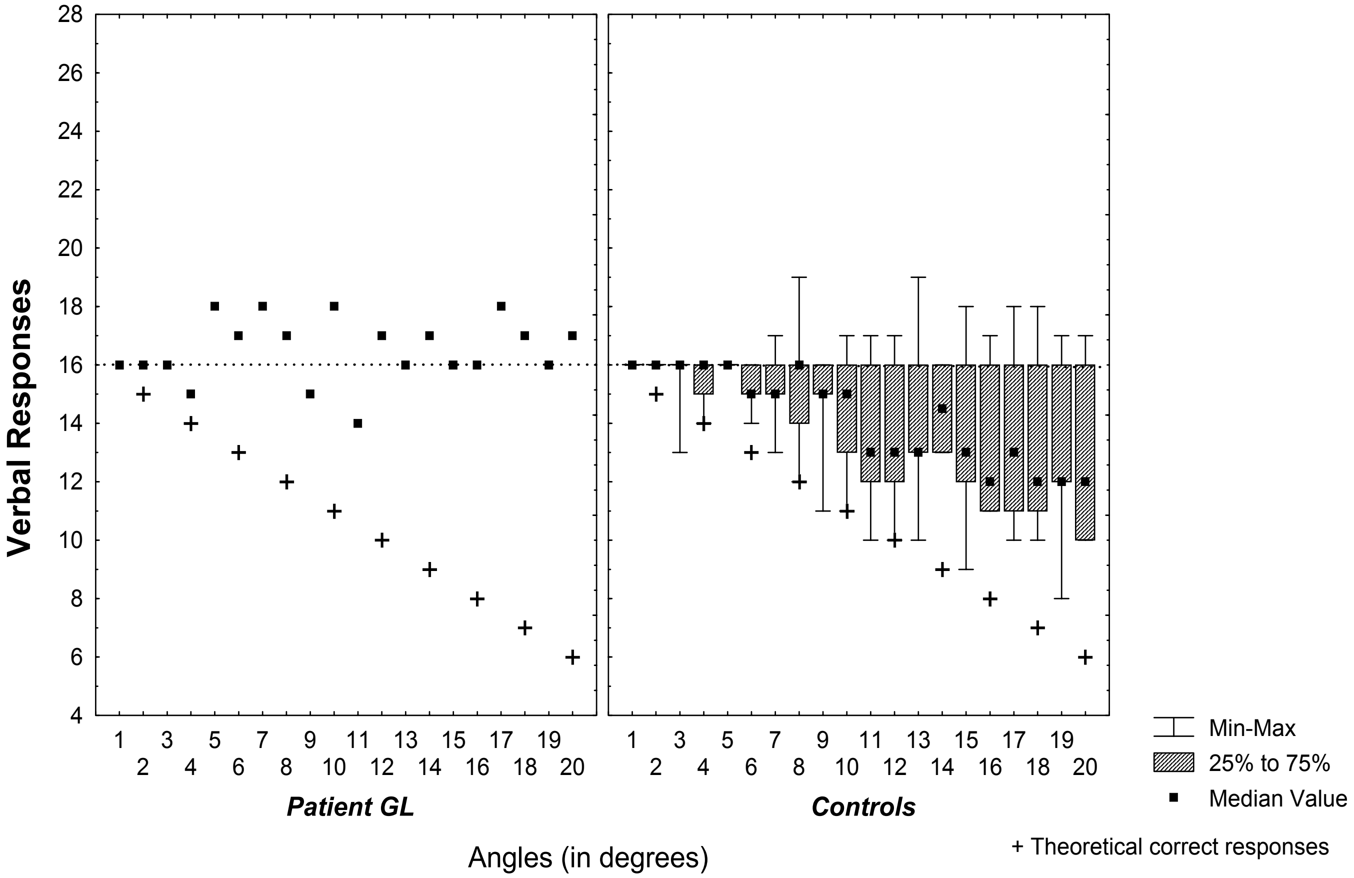

Fig. 2

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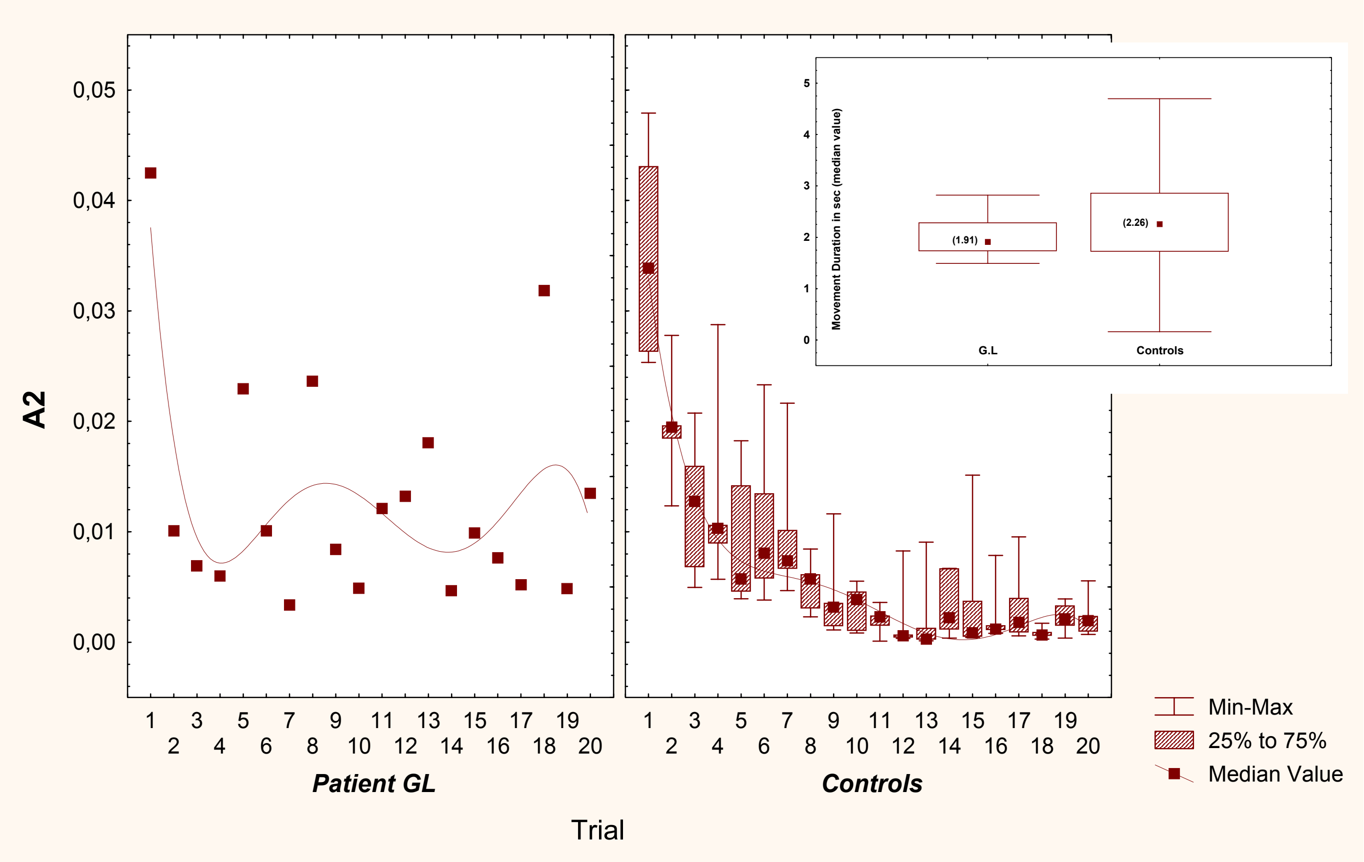

Fig. 3

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Fig. 4

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