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Inferring another's expectation from action: the role of peripheral sensation

Simone Bosbach[1], Jonathan Cole[2], Wolfgang Prinz[1] & Günther Knoblich[3]

It is unclear how knowledge of one's actions and one's body contribute to the understanding of others' actions. Here we show that two subjects lacking cutaneous touch and sense of movement and position show a selective deficit in interpreting another person's anticipation of weight when seeing him lifting boxes. We suggest that this ability occurs through mental simulation of action dependent on internal motor representations, which require peripheral sensation for their maintenance.

Successful social interaction depends on an ability to understand others' actions in relation to intentions and expectations. In turn, the interpretation of others' actions seems to require both observation of the other and a form of motor knowledge[1]. More precisely, action recognition seems to involve the direct mapping of a perceptual representation of a particular observed action onto a representation of the appropriate motor pattern for the same action in the observer. This suggests that, at some level, interpretation of observed action requires simulation[1,2], including a central representation of the observer's body[3]. The role of peripheral sensation in this process has not yet been explored. Here we show that two subjects who have lost the senses of cutaneous touch and proprioception show a specific deficit in understanding the expectations of another person when seeing him lifting boxes of differing weights. Thus, peripheral sensation from one's own body may contribute to inferences about certain mental states of other people derived from observing their actions.

The hypothesis that proprioception informs the understanding of another's expectation in relation to a particular action was tested in two subjects, GL and IW, who live with the extremely rare condition of selective and complete haptic deafferentation due to a sensory neuronopathy. Both have lost cutaneous touch and proprioception from their body, either below the head (IW) or nose (GL)[4,5]. They observed videos of control subjects (**Fig. 1**) lifting a large (3, 6, 12 or 18 kg) or small (0.05, 0.3, 0.6 or 0.9 kg) box. In the first task, GL and IW were asked to estimate the weight of the box lifted by the subject, who was always given correct information of that weight[6,7] (compare with refs. 5,8). In the second task, they were required to judge whether the

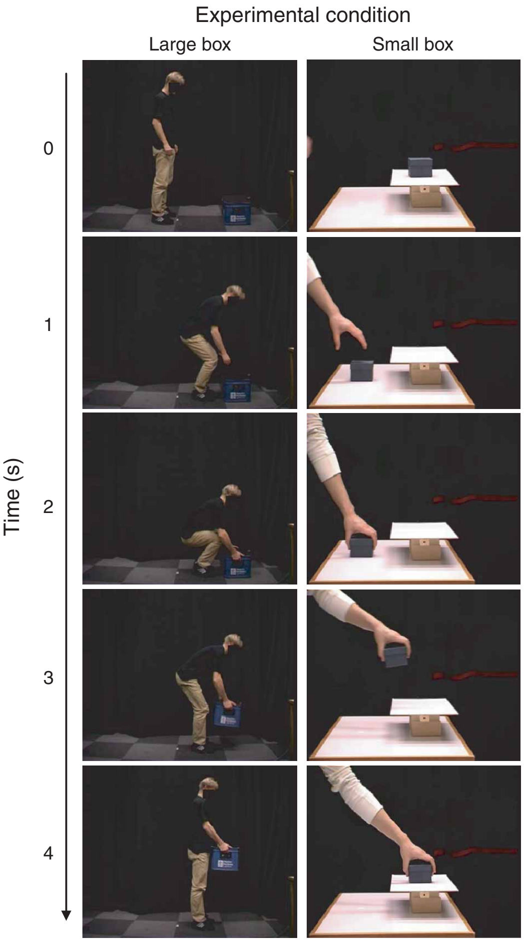

Figure 1 Video recording. Two naive subjects (male and female) were recorded lifting a large or small box, each of four different weights. Lifters were told the correct weight of the box before lifting it. On eight random occasions out of 48 trials, this information was false; that is, lifters were deceived about box's weight. The large and small box conditions varied the saliency of visual cues. Each movie in the large box condition showed the lifter going up to a box and lifting it. Lifters' faces were blacked out to hide facial emotional expressions. Each movie in small box condition showed the lifter's arm lifting and placing a box on a shelf. Trials in the large and small box condition of the weight expectation judgment task were made up of all possible combinations of two lifters (male, female), four weights, two instances and four repetitions, randomly intermixed. Respectively, all trials of expectation judgment task were made up of two lifters (male, female), four weights, two weight expectations (correct, false) and four repetitions, randomly intermixed. Informed written consent was obtained from each subject.

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[1]Department of Psychology, Max Planck Institute for Human Cognitive and Brain Sciences, Amalienstr. 33, 80799 Munich, Germany. [2]University of Bournemouth and Poole Hospital, Clinical Neurophysiology, Longfleet Road, Poole, BH15 2JB, UK. [3]Psychology Department, Rutgers University, 101 Warren Street, Newark, New Jersey 07102, USA. Correspondence should be addressed to S.B. (bosbach@cbs.mpg.de).

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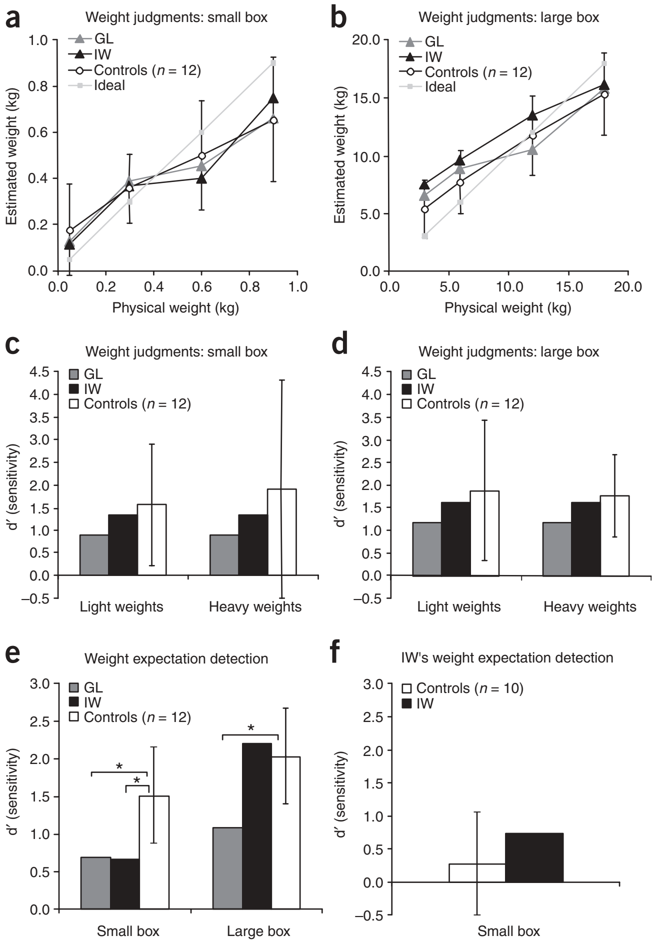

Figure 2 Results. (**a**,**b**) Perceived weight of lifted box increased proportionally to its physical weight. *t*-tests on each slope coefficient of linear regressions for controls differed significantly from zero in small box condition (**a**; mean $\beta = 0.55$; range 0.20–0.76) and large box condition (**b**; mean $\beta = 0.66$; range 0.41–0.80; P values < 0.001). Weight judgments were more accurate in the large than in the small box condition ($P < 0.05$, $t = 2.77$). GL's slopes for small and large box condition were $\beta = 0.58$ and $\beta = 0.57$, respectively; IW's were $\beta = 0.68$ and $\beta = 0.58$, respectively. Performance of GL and IW individually, compared against controls[15], was in the normal range (P values > 0.3). (**c**,**d**). d′ sensitivity measures for weight judgments. Neither IW's nor GL's performance in discriminating light weights in the small and large box conditions (0.05 and 0.3 kg, 3 and 6 kg, respectively) differed significantly from controls (for 1 s.d., all P values > 0.36). The same was true for heavy weights in both conditions (0.6 and 0.9 kg, 12 and 18 kg, respectively; for 1 s.d., all P values > 0.24). (**e**) d′ sensitivity measures for expectation judgments. Controls were able to correctly detect lifter's expectations in the small (mean d′ = 2.03; range d′ = 1.50–2.47) and large box condition (mean d′ = 1.51; range 1.04–2.27; all d′ values were significantly above chance; P values < 0.001). The difference between the small and large box conditions was significant ($P < 0.01$, $t = 4.25$). Judgments regarding lifter's expectation were more accurate in the large box condition. GL's accuracy was significantly reduced in the large box condition: d′ = 0.69 ($P = 0.0.032$, $t = -2.46$) and the small box condition; d′ = 1.09 ($P = 0.017$, $t = -2.82$). The same was true for IW's performance in the small box condition: d′ = 0.66 ($P = 0.027$, $t = -2.55$) but not in the large box condition, d′ = 2.21 ($P = 0.6$). (**f**) Results of IW's expectation judgments. Controls were less accurate in detecting IW's expectations (mean d′ = 0.27; range d′ = –0.33 to –0.98) than IW was himself (d′ = 0.73, but the difference was not significant, $P = 0.29$).

subject observed had been given correct or incorrect information of the box's weight before lifting it[9].

These tasks require deriving a hidden state from the kinematics of an observed action, which in turn depends on both the information given to the lifter and the weight encountered. If the weight is as expected, detecting differences between actions tailored to different anticipated weights is sufficient for the observer to infer the object's weight. GL and IW are able to correctly identify such differences when they observe their own actions[4,8]. However, in order to determine whether the lifter was deceived about the given weight, an observer needs to recognize mismatches between the prepared and the resulting movement.

We compared GL's and IW's performance with the performance of matched controls to determine whether intact peripheral sensation from one's own body is necessary for detecting such mismatches: if it were necessary, we would expect GL and IW's performance to be impaired when they judged the expectation of the lifter, but not when they judged the weight of the lifted object. We found that GL and IW's ability to judge the weight of small and large boxes was well within the normal range (**Fig. 2a–d**). Their lack of peripheral afferents did not affect their ability to distinguish between various weights when the subjects' expectations were correct. In contrast, in the small box condition of the weight expectation task, GL and IW's accuracies were clearly below that of any of the 12 controls (mean age 50.9 ± 8.1 years; three males) whether the weight expectation observed was correct or false. For GL, the same was true in the large box condition. IW, however, was able to use the more salient cues in this condition to achieve a detection rate comparable to controls. Controls were significantly more accurate in the large box than in the small box condition, suggesting that additional visual cues were present in the

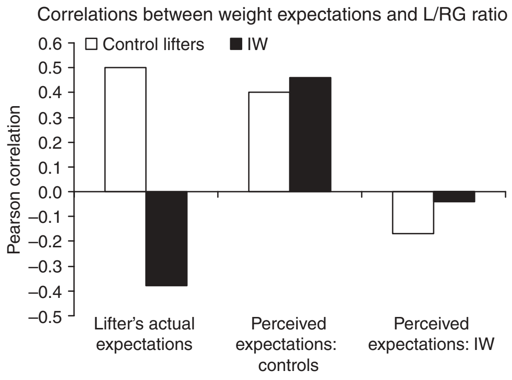

Figure 3 Movement kinematics and weight expectations in the small box condition. In movies displaying control lifters, relative duration of the lift phase (L/RG) provided the most informative hint as to whether the lifter's expectation matched actual weight. The higher the L/RG, the more likely that the lifter's expectation was actually wrong. Controls used this covariation to judge the control lifter's expectation from movement kinematics. The higher the L/RG, the more likely that they perceived the lifter's expectation to be wrong. In contrast, IW was not able to use this covariation to infer the control lifter's expectation. In movies of IW, the relationship between L/RG and his actual expectations was reversed. The lower the L/RG, the more likely he had the wrong expectation. However, controls still perceived movements with higher L/RG as reflecting a wrong expectation. Thus, they interpreted IW's movements in the same way as those of any other lifter. As in the observation of movies of control lifters, L/RG did not influence IW's judgment of his own expectations.

large box condition (**Fig. 2e**). Together, these results indicate that a lack of touch and/or proprioceptive afferents significantly reduces the ability to recognize others' expectations of weight.

These results suggest that GL and IW have a selective deficit in detecting a match or mismatch between another's prepared and resulting movements. However, this first experiment could not untangle whether this deficit was due to the sensory loss or to a deficit in action execution. To distinguish between these two, we asked IW to pick up the small boxes himself, recorded him and then showed these videos to him and to controls. (IW could not perform the large box condition). This also allowed us to avoid the criticism that what we had identified was not a reduced ability to deduce expectation from action, but a more general problem in recognizing action.

IW was no more accurate when he judged his own weight expectations; visual familiarity with his own movement patterns did not improve his ability to infer expectation (**Fig. 2f**). The accuracy of ten healthy controls (mean age 48.1 ± 5.5 years; five males) in judging IW's expectation was close to chance. They could not use differences in IW's movements to infer his having a correct or incorrect weight expectation. Since he picked up the weights, this also showed that IW's deficit in the weight expectation judgment task was not due to a deficit in execution.

To corroborate our assumption that recognition of the lifter's expectation depends on the degree of match between prepared and resulting movement, we measured several kinematic parameters from the movies of control lifters and IW lifting small boxes of expected and unexpected weight. The best predictor of false weight expectation in controls was the duration of the lifting phase of the movement divided by the sum of the duration of the reaching phase and the grasping phase (that is, relative lifting duration or L/RG; **Fig. 3**). The larger L/RG, the greater the likelihood that a control's weight expectation was wrong. IW, in contrast, showed an inverse relation between L/RG and weight expectation. Thus, IW's movements differed from the control's in kinematics that allow one to recognize false weight expectations.

Controls perceived lifters' weight expectations as being wrong when L/RG was large (**Fig. 3**). This explains why their judgments were accurate for fellow controls but not accurate for IW; a large L/RG was a valid predictor of controls' false expectations, but it was not for IW's. In contrast, L/RG did not influence IW's judgments of an observed lifter's weight expectations, regardless of whether he observed controls or himself.

Understanding an observed subject's expectation requires judgment of mismatches between prepared and resulting movements when that expectation is wrong. In the present task, such mismatches increased the relative duration of the lifting phase of the movement, presumably reflecting readjustments during this phase. The first experiment demonstrates that the two subjects' deafferentation reduced their ability to interpret these adjustments as an indicator of the other's expectation. The second experiment shows that IW's deficit in the weight expectation task was not due to a general deficit in execution. However, his movements did not provide useful cues for him or controls to identify his weight expectations. IW and GL do not receive peripherally originating sensory feedback of movements they perform, either at a perceptual level or at the subperceptual level required for motor control (compare ref. 10). Their reduced ability in the present task suggests that to judge mismatches between action preparation and performance in others, one has to access subconscious sensorimotor programs, which IW and GL may lack. It seems unlikely that this recognition of postural adjustments requires an ability to make and perceive similar small movements in oneself, since subjects did not move during the task. We therefore suggest that this task requires an implicit internal simulation, possibly by means of motor programs. Since IW was able to lift the boxes in the second experiment, he can construct an internal motor representation of the action, though phenomenologically this involves conscious supervision of a different degree to controls.

It is known that both GL and IW have limited and transient motor memory[11,12], but they do not seem to be able to access, implicitly or explicitly, internal motor representations to simulate the present task. Without sensory feedback to update and maintain them, such representations may decay. The difference between IW's and GL's performances in the large box condition of the expectation judgment task parallels IW's larger movement repertoire which, in turn, suggests his development of more feed-forward motor planning. More generally, peripheral sensation may not only have a role in identifying some emotions in others (compare refs. 13,14) but may also be necessary to understand another's action following expectation. Without such feedback, the internal models upon which such understanding depends are either no longer accessible or extant.

COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

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