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Illusions of Force Perception: The Role of Sensori-Motor Predictions, Visual Information, and Motor Errors

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[1]*Wolfson Center for Cognitive Neuroscience, School of Psychology, University of Wales, Bangor, United Kingdom;* [2]*W. M. Keck Foundation Center for Integrative Neuroscience, Department of Physiology, University of California, San Francisco;* [3]*Department of Psychology, University of California, Berkeley; and* [4]*Helen-Wills Neuroscience Institute, University of California, Berkeley, California*

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Diedrichsen J, Verstynen T, Hon A, Zhang Y, Ivry RB. Illusions of force perception: the role of sensori-motor predictions, visual information, and motor errors. *J Neurophysiol* 97: 3305–3313, 2007. First published March 7, 2007; doi:10.1152/jn.01076.2006. Internal predictions influence the perception of force. When we support an object with one hand and lift it up with the other, we expect the force to disappear from the first, postural hand. In a virtual reality system, we violated this prediction by maintaining the force on the postural hand, whereas the object was still seen and felt to be lifted by the lifting hand. In this situation, participants perceived an illusionary increase in force on the postural hand, which was, in reality, constant. We test three possible mechanisms of how force perception may be influenced in this context. First, we showed that part of the illusion can be linked to a sensorimotor prediction—the predicted sensory consequences based on an efference copy of the lifting action. The illusion is reduced when the object is lifted by an external force. We also showed that the illusion changes on a trial-by-trial basis, paralleling the fast adaptation of the postural response. Second, motor errors that arise from a miscalibrated forward model do not contribute to the illusion; the illusion was unchanged even when we prevented motor errors by supporting the postural hand. Finally, visual information signaling the removal of the object is sufficient to elicit part of the illusion. These results argue that both sensorimotor predictions and visual object information, but not motor errors, influence force perception.

INTRODUCTION

The perception of forces that act on the body is influenced by our expectations. The football player who sees the approaching opponent is likely to anticipate the tackle and perceive the impact as less jolting than the player who is tackled with similar force from an unseen angle. Predictions about forces can arise from observation of external agents and from the experience with consequences of our own action; furthermore, these predictions in turn alter our own motor output. To study how these factors contribute to the perception of force, we explored a new illusion, in which a change in force is experienced even though the force, in reality, is constant.

We discovered this illusion accidentally during a series of experiments studying the dynamics of bimanual coordination (Diedrichsen et al. 2003, 2005a). Using a virtual reality system, participants supported an object in one hand, the postural hand (Fig. 1*A*) and, when cued, lifted it with the other hand, the lifting hand (Fig. 1*B*). The visual feedback of the rising object and the forces that acted on the lifting hand were always veridical. However, on a small percentage of trials, the load force of the object remained on the postural hand as the object was lifted. In this situation, participants perceived a strong increase in the force acting on the postural hand, although the true load force remained constant.

This misperception is similar to a number of related illusions, all of which have in common the influence of internal predictions on the actual sensory data. In the classic size-weight illusion, we expect a larger object to be heavier than a smaller object. When both objects have the same weight and are lifted, the larger object is perceived to be lighter (Charpentier 1891). Another example comes from the recent work of Bays et al. (2005, 2006) and Shergill et al. (2003). Force pulses applied to the fingers were judged to be stronger when they were externally generated rather than when the same forces were the consequence of self-produced actions. In this case, the voluntary action seems to give rise to a detailed prediction about the sensory inflow, and in the absence of this prediction, the force is perceived to be stronger.

What are the mechanisms by which these internal predictions influence the perception of force? Considering the force illusion we observed in our lifting task, we can identify three possibilities. First, the illusion may arise because our sensorimotor system continuously generates a prediction concerning the expected sensory consequences of self-produced actions (Fig. 2*A*), and this prediction is compared with the sensory inflow (Blakemore et al. 1998). A violation of the prediction, as would occur when the force on the postural hand is maintained, may be misperceived as an increase in force. In the unloading task, this sensorimotor prediction is directly observable: it results in a reduction in the upward force generated by the postural hand at the time of unloading, an anticipatory response that allows the postural hand to remain stable (Hugon et al. 1982). This anticipatory response is not generated when the object is lifted by an external agent, even if this event is highly predictable, and extensive training is provided (Diedrichsen et al. 2003). Thus following this hypothesis, the misperception of force should only be present when the object is lifted with a self-generated action. Furthermore, we have shown that the postural response is modified immediately after a catch trial (Diedrichsen et al. 2005b). If this adaptation changes the predictive forward model that also influences force perception, the illusion should also be modulated in a similar trial-by-trial fashion.

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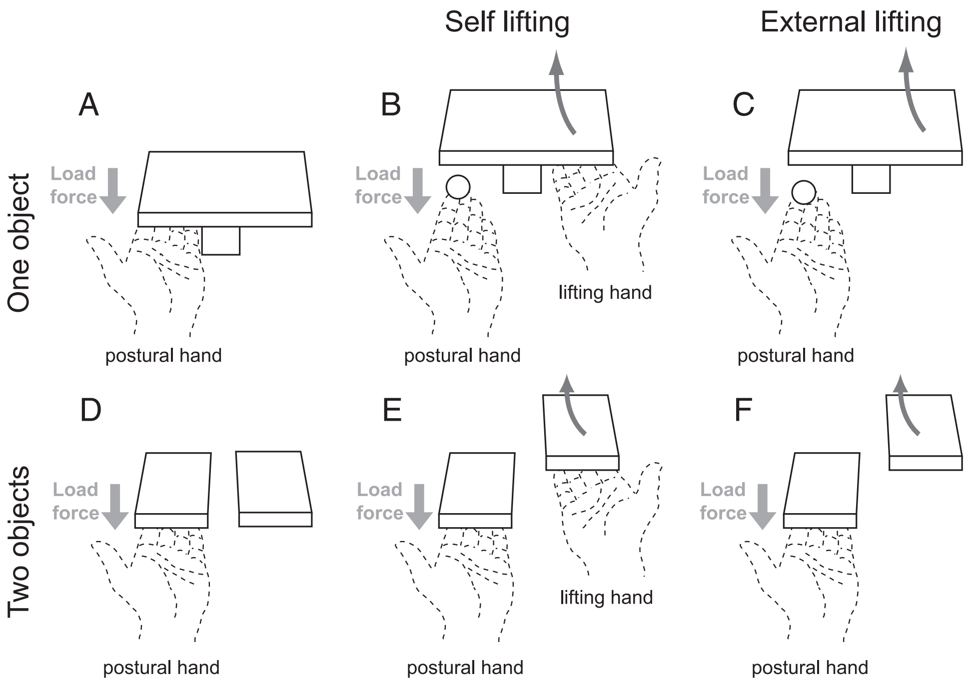

FIG. 1. Force illusion during unloading task. *A*: participants hold an object with the postural hand. *B*: object is lifted by the participant using the other, lifting hand. A virtual environment was used to simulate forces to hands. When load force of object remains on the postural hand, even after object is lifted, a sudden increase in force is perceived. Participants could not see their hand during the task, but small spheres symbolized location of their index fingers. *C*: during external lifting, a simulated force lifts object from postural hand. *D–F*: to manipulate the visual information about object, a part of the object remains on the postural hand during 2-object condition (*experiment 2*).

Second, the unintended movement of the hand itself, the motor error, may lead to the illusion. A displacement of the postural hand during unloading occurs when the postural response is not correctly matched to the actual force change on the hand (Fig. 2*B*). A downward perturbation accompanied by the stretch of the muscles may be interpreted as an increase in the force acting on that hand. This hypothesis would predict that the illusion would only be present when motor errors are present.

Third, the illusion may arise because the brain attempts to make sense of the sensory input, attributing sensations to possible causes based on conceptual knowledge and the visual context (Fig. 2*C*). From experience, we know that supported objects exert load forces. When the attributed cause of the force is removed (e.g., the object is lifted), a persistent force on the postural hand may be perceived to become heavier because that force has no known source (for a similar argument of how causal attributions influence perception, see Haggard et al. 2002). In contrast to sensorimotor predictions, this interpretation may influence the percept after the fact, because visual information about the lifted object arrives at the brain later than proprioceptive information. This hypothesis would predict that the visual presence or absence of an object on the hand determines the size of the force illusion. Therefore the illusion should be just as strong when an object is lifted by an external force as when it is lifted by the person's other hand (Fig. 1*C*), and the illusion should be absent when the object is visually perceived to remain on the hand (Fig. 1, *D–F*).

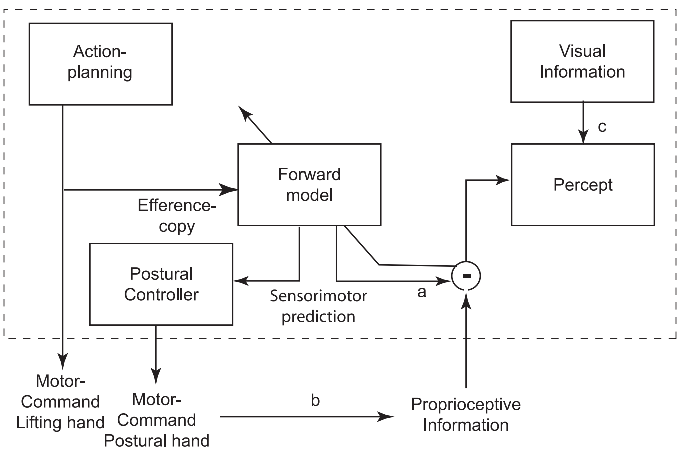

FIG. 2. Possible causes for force illusion. *A*: efference copy of motor commands in self-lifting condition is used by a forward model to generate a sensorimotor prediction. This prediction is directly compared with sensory input, and discrepancy influences perceived force. *B*: the sensorimotor prediction is also used by a postural controller to issue an anticipatory postural response. This can lead to a motor error, a downward perturbation of the postural hand on sustained trials. This, in turn, changes the proprioceptive input and may be perceived as an increase in force. *C*: visual information about the object may alter the perceived force.

Here, we evaluate the contribution of these three possible causes to the force illusion in the unloading task. In *experiment 1*, we compared the perception of force when the object was lifted by the other hand (i.e., volitional action) to a condition in which the object was lifted externally. If sensorimotor predictions are at least partly responsible for the illusion, the force should be perceived to increase more strongly in the self-lifting than in the external lifting condition. Also, to determine whether the occurrence of motor errors alters force perception, we compared conditions in which the postural hand was either unsupported or rested on a supporting surface. The latter condition eliminates the anticipatory response of the postural hand and the occurrence of motor errors.

In *experiment 2*, we evaluated the influence of visual information of the object on force perception using two manipulations. First, we only used trials in which the force was sustained on the postural hand, leading to a rapid adaptation of sensorimotor predictions. In this manner, we effectively eliminated the influence of sensorimotor predictions on force perception. A similar strategy was used by Flanagan and Beltzner (2000) in the context of the size-weight illusion. In their experiment, participants repetitively lifted small and large objects of the same weight. Initially, small objects were lifted with less grip force than large objects. However, the sensorimotor prediction adapted quickly: after a few lifts, participants produced identical grip forces for small and large objects. Nonetheless, the size-weight illusion persisted, indicating that visual information about the object rather than sensorimotor predictions caused the illusion.

Second, we manipulated the visual information directly. In one condition, the whole object was lifted, creating the expectation that the load should disappear. In a second condition, the object consisted of two parts, one of which remained on the postural hand (Fig. 1, *D–F*), creating the expectation that the force should remain constant. To the degree to which the interpretation of visual information leads to an illusory percept, the force should be perceived to increase more in the one-object than in the two-object condition, even in the absence of erroneous sensorimotor predictions.

METHODS

Participants

Ten participants were recruited for *experiment 1* (4 male; mean age = 22.8 yr; 1 left handed) and 24 participants (15 male; mean age = 19.2 yr; 3 left handed) were recruited for *experiment 2*. All participants were recruited from the University of California Berkeley community. Participants were naïve to the purpose of the study and either received course credit or monetary compensation for their participation. The experimental protocol was approved by the Institutional Review Board of UC Berkeley.

Apparatus and stimuli

A virtual three-dimensional (3D) environment was created in which participants could interact with objects. Participants viewed a virtual scene that was presented on a 22-in computer monitor and reflected through a mirror such that it appeared to be in the natural manual workspace directly in front of the participant's chest. Within the 40 × 26 × 35-cm workspace (width, height, depth), a virtual object, consisting of a platform (20 × 2 × 10 cm) and stand (3.5 × 7 × 3.5 cm), was visible (Fig. 1, *A–C*). Although the participants could not see their hands, the position of each hand was indicated by a 1-cm-diameter sphere. By calibrating the visual display to robotic devices linked to each hand, the 3D location of the spheres reflected the vertical position of the index fingers. Index and middle finger of each hand were yoked together and linked to the end of a robotic arm (PHANToM 3.0 System, SensAble Technologies). The robotic system allowed us to simulate forces that would be experienced as the person interacted with a 400*g* object, creating the convincing impression of an interaction with a real object.

Experiment 1 procedure

Participants in *experiment 1* underwent two testing sessions, conducted on separate days. In one session, the postural hand was unsupported. Participants began each trial by holding their hands, palms facing upward, below the object. When cued, they lifted the object with the postural hand and held it at a visually specified height, 4–7 cm above the floor of the workspace (Fig. 1*A*). In self-lifting trials, a sound was played after 500 ms instructing participants to lift the object with their other hand (Fig. 1*B*). Participants were trained to lift the object with a smooth motion, bringing it to a height ≥13 cm above the workspace floor, and to hold the object in this new position. In external lifting trials, the object was lifted by a computer-generated force, while the lifting hand rested in the lap of the participant. The timing of this force was fixed and approximated the time-course of unloading in the self-lifting trials (Fig. 1*C*). For both self- and external lifting trials, the participant judged whether the force on the postural hand had increased or decreased during the lifting of the object. This judgment was made relative to external lifting trials that were presented as standards at the beginning of each block (see *Perceptual judgments*). The response was made as soon as the object had been moved to its final position. The instructions emphasized that the responses were to be only based on the change in the force acting on the postural hand. Participants were instructed not to judge the weight of the object or the force exerted on the lifting hand.

In the other session, the postural arm was supported by a wooden platform positioned 4–7 cm over the floor of the workspace. Participants were instructed to keep the arm relaxed for the entire trial, with the object passively resting on the supported postural hand at the start of each trial. All other aspects of the supported trials were the same as for the unsupported trials. The object was lifted, either by the participant's other hand or by the computer, and a judgment was made about the force acting on the postural hand after the object was lifted.

For a given trial, force feedback on the postural hand either simulated natural unloading or a sustained force. For unloading trials, the load force of the object reduced to zero, corresponding to the upward movement of the object. The force was calculated based on the contact of the hand with the object, using a stiff spring (580 N/m) as a model for the object surface. For sustained trials, the force presented to the unloading hand was a scaled version of the force that would have been experienced on an unloading trial. Therefore these trials showed the same time-course of force change as natural unloading trials, only the amount of force changed varied between −20% and +20%, with natural unloading trials showing a force change of −100%. For example, if the lifting action would have reduced the load force on the postural hand at time t from 5 to 1 N on an unloading trial, the presented force on an sustained trial would be 5 N − 0.2(5 N − 1 N) = 4.2 N for a −20% trial, 5 N + 0.2(5 N − 1 N) = 5.8 N for a +20% trial, and 5 N for a 0% trial.

Because the sensorimotor prediction and the anticipatory response are quickly attenuated after sustained trials (Diedrichsen et al. 2005b), we included a majority of natural unloading trials to ensure that participants maintained a sensorimotor prediction. Each block was composed of 20 unloading trials and 10 sustained trials, randomly intermixed.

In each session, participants completed 20 blocks, alternating between self- and external lifting blocks. The postural hand switched after each pair of self- and external lifting blocks. No differences in judgments were observed between the two hands; thus we collapsed the data across hands in the analyses. The sequence of trials for the unsupported and supported sessions was identical. The first four blocks were practice blocks to allow the participants to become familiar with the VR environment and unloading task. No force judgments were made during these blocks. One half of the participants started with the unsupported session and the other half with the supported session.

Experiment 2 procedure

One half of the participants were assigned to the one-object condition and the other half to the two-object condition. In the one-object condition, the visual display and trial procedure were identical to the unsupported condition of *experiment 1*. In the two-object condition, the display contained two objects, each consisting of a platform 7.5 cm in width. The two objects, one on the left and one on the right side, were separated by a gap of 5 cm.

In the two-object condition, the object on the opposite side of the postural hand was elevated 5 cm above the virtual floor at the beginning of the trial. The participant lifted the other object with the postural hand to the same height (Fig. 1*D*). During both external and self-lifting trials, the supported object remained on the postural hand, whereas the other one was lifted (Fig. 1, *E* and *F*). Thus the participant saw that the object remained on the postural hand while experiencing the same forces (including the force change) as in the one-object condition.

Participants completed 16 blocks of 21 trials each, all involving sustained load force. No unloading trials were presented in this experiment. As in *experiment 1*, participants judged whether the force on the postural hand increased or decreased relative to that perceived before the object was lifted. The weight of each object was set to 350 g, and the simulated force changes ranged from −30% to +30% in steps of 10%. The first four blocks were practice blocks and did not involve force judgments.

Perceptual judgments

Participants responded verbally whether they perceived the sustained force on the postural hand as "heavier" or "lighter" relative to the load force generated by the object before lifting. They were also allowed to report that they perceived no sustained force, the correct response on normal unloading trials. The participants' verbal force judgments were entered into the computer by the experimenter. For the sustained trials, these responses were modeled separately for each participant and condition using a logistic regression model

$$\log\left[\frac{\mathrm{p(increased)}}{1-\mathrm{p(increased)}}\right] = \theta_0 + \theta_1 x_1$$

where *p*(increased) is the probability for each trial that the participant judges the force to have increased, x_1 is the actual force change, and θ_i is the regression coefficient. The point of subjective equality (PSE) can be calculated as PSE $= -\frac{\theta_0}{\theta_1}$. To study the influence of the sensorimotor prediction onto force perception on a trial-by-trial basis, we re-estimated the model after adding the additional regression term $\theta_2 z_n$, where z_n represents the size of the sensorimotor prediction on that trial (see RESULTS for details).

For the mixture of natural unloading trials and sustained trials in *experiment 1*, pilot data showed that participants were inclined to judge any sustained force as an increase over that experienced before unloading. This bias presumably arose because of the significant across-trial contrast between unloading and sustained trials. To overcome this bias, we presented two reference trials, labeling one "a decrease " and the other "an increase " at the start of each block of trials, using external lifting conditions with a force change of −20% or +20%, respectively. We indicated to participants that they should judge the force change with these standards in mind. Therefore the perceptual judgments were made relative to the external lifting condition. Thus only the difference between psychometric curves, but not their absolute values, could be interpreted in *experiment 1*.

In *experiment 2,* only sustained trials were presented, making reference trials at the start of each block unnecessary. This also meant that both the difference in the psychometric functions and the absolute values of these functions (PSE) were interpretable.

Kinematic data

To assess the size of the anticipatory response of the postural hand, we recorded the position of the postural hand and the forces produced by the robotic device at 200 Hz. Acceleration was computed by double numerical differentiation of position data and smoothed with a 12-ms FWHM (full width at half maximum) Gaussian kernel.

RESULTS

Experiment 1

Experiment 1 was designed to dissociate the influence of sensorimotor predictions and motor errors on force judgment. Participants either lifted the object using the hand that was not supporting the object (self lifting) or the object was removed at an unpredictable time by the computer (external lifting). Sensorimotor predictions should only be present during self-lifting. To manipulate motor errors, we compared the unsupported and supported condition. The visual information concerning the object during both conditions was essentially identical.

ANTICIPATORY POSTURAL RESPONSE. Figure 3 shows the average load force and velocity for the postural hand in the self-

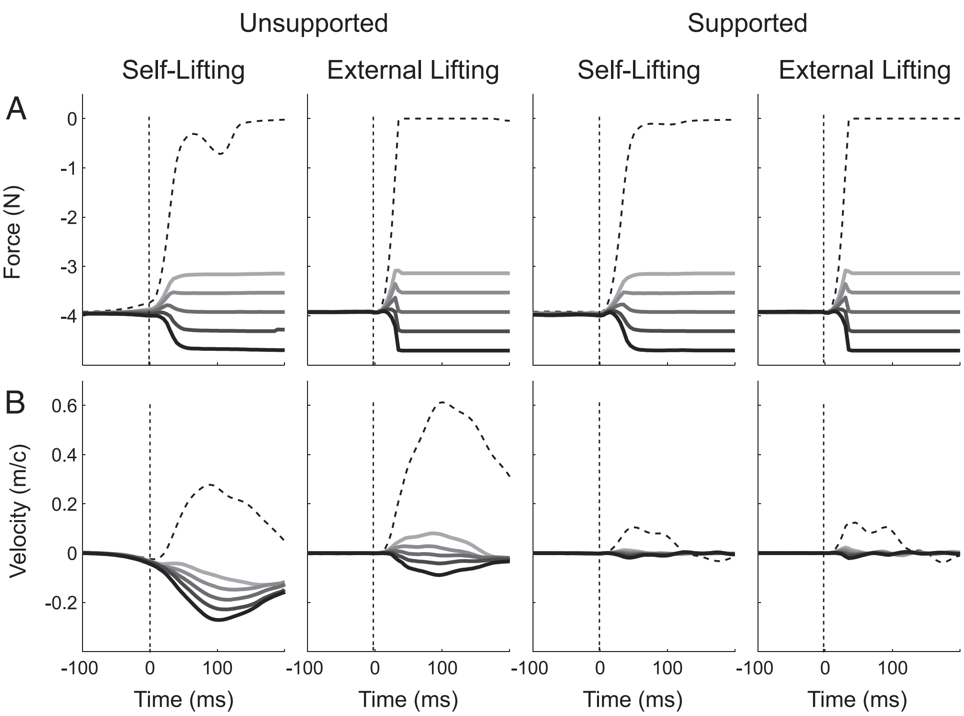

FIG. 3. Behavior of postural hand during self- and external lifting. *A*: time-course of force acting on postural hand, averaged over all participants. Data are combined across trials in which the left or right hand was used to support object. Negative numbers indicate downward forces. Force either disappeared completely (−100%, natural unloading; dashed line) or changed by an amount between −20% and +20%. All traces are aligned to beginning of unloading (0 ms)—time-point when force begins to be applied to the object by the lifting hand or external force. *B*: velocity (positive number indicates upward movement) of postural hand. Reduced upward movement in unsupported self-lifting condition indicates anticipatory response.

and external lifting conditions for the unsupported and supported session. The load force was removed very rapidly during self-lifting (median, 44 ms) and during external lifting (35 ms). The difference between the self- and external lifting conditions was reliable [$t(9) = 4.486$, $P = 0.002$]. There were no significant differences between the supported and unsupported trials in the speed of unloading.

The velocity traces (Fig. 3*B*) of the postural hand indicate an anticipatory postural response in the unsupported condition. During trials in which the weight was completely removed, the hand showed an upward perturbation during external lifting. This perturbation was substantially reduced during self-lifting. Here, the postural hand showed an anticipatory downward movement, beginning ~50 ms before the start of lifting, indicative of an anticipatory reduction of the upward force (Diedrichsen et al. 2005b).

The results of the sustained trials provide further evidence for an anticipatory response: during external lifting, the postural hand moved upward when the load force decreased and downward when the load force increased (Fig. 3*B*). During self-lifting, all sustained trials showed a downward perturbation, with the magnitude related to the size of the force change.

On supported trials, the postural hand did not move. The residual velocity on unloading trials is an artifact caused by the fact that the link between the hand and robotic device was not perfectly stiff. Therefore when the load force on the hand reduced, the robot arm moved slightly upward, stretching the link between robot arm and human hand. However, most importantly, the velocity of the robot arm did not differ between the self- and external lifting conditions, indicating the absence of an anticipatory postural response.

To obtain a measurement of the size of the anticipatory response, we plotted the average acceleration of the postural hand against the force imposed on that hand (Fig. 4*A*). This calculation was averaged over the time interval from −25 ms before until 50 ms after the start of lifting to exclude feedback-based adjustments. During external lifting, the hand behaved like a passive object; the acceleration was linearly related to the force acting on the hand in that period. The slope of this line provides an estimate of the effective inertia of the hand (Fig. 2*B,* dashed line; see also Diedrichsen et al. 2005b). During self-lifting, acceleration was systematically more negative than for the same level of force during external lifting. Thus the upward force produced by the postural hand must have been reduced during self-lifting, a manifestation of an anticipatory response. The size of this reduction can be estimated by taking the horizontal distance from the self-lifting force to the external lifting regression line, i.e., the force that resulted in the same acceleration during external lifting. This distance provides a measure of the anticipatory response for individual trials.

The size of the anticipatory response varied from trial to trial. This is because the sensorimotor system rapidly adapted to errors in the prediction on the previous trial (Diedrichsen et al. 2005b). Figure 4*B* shows the average size of the anticipatory response plotted as a function of whether it preceded or followed a sustained trial. After a sustained trial, the anticipatory response was significantly reduced and returned to baseline only after a number of natural unloading trials.

This fast adaptation can be modeled using a state-space model of sensory motor learning (Donchin et al. 2003). This allows us to estimate the sensorimotor prediction on each trial given the history of actual force changes, a result that will be useful in our analysis on the influence of sensorimotor predictions on perceptual judgments. In this model, the size of the anticipatory response on each trial n, y_n, depends on the sensorimotor prediction, i.e., the predicted change in force, on that trial, z_n. Over the course of the experiment, the participant experienced a series of actual force changes, $u_1 \ldots u_N$. We reasoned that the participant would predict on average the average force change, i.e., $\bar{z} = \bar{u}$. We further assumed that when an individual predicted no force change, i.e., $z = 0$, they would not show any anticipatory response, from which follows

$$y_n - \bar{y} = \frac{\bar{y}}{\bar{u}}(z_n - \bar{u})$$

We proposed that the sensorimotor prediction on the next trial (z_{n+1}) is a combination of the last sensorimotor prediction and the prediction error on the last trial ($u_n - z_n$)

$$z_{n+1} - \bar{u} = A(z_n - \bar{u}) + B(u_n - z_n)$$

The parameter B expresses how fast the prediction adapts to new sensory experiences; the parameter A determines how fast the prediction drifts back to the average prediction if no errors are present. We estimated the model parameters A and B by minimizing the sums-of-squares between predicted and actual anticipatory response. The average A was 0.958 ± 0.056 (SE) and the average B was 0.379 ± 0.037, which was highly significantly different from zero [$t(9) = 9.744$, $P < 0.001$]. Thus the participants showed significant trial-by-trial adaptation of the anticipatory response.

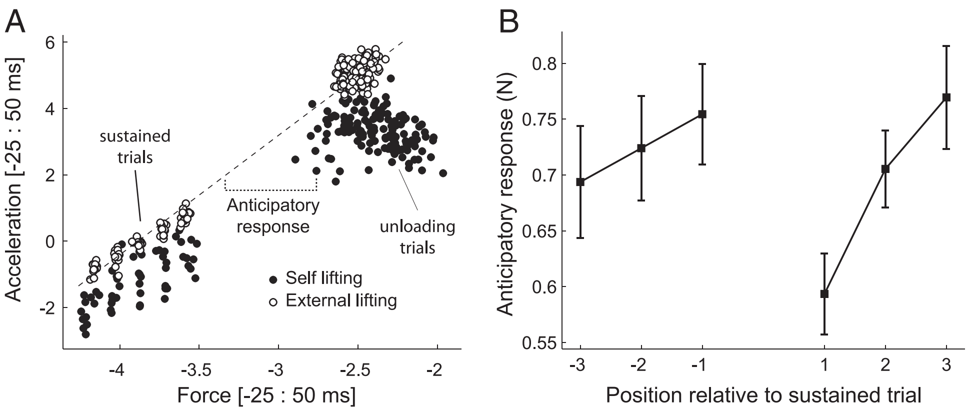

FIG. 4. Anticipatory postural adjustments in *experiment 1*. *A*: acceleration of postural hand plotted as a function of force acting on postural hand for a representative participant. Large right cluster shows results for natural unloading, whereas the 5 smaller clusters show results for 5 levels of force change during sustained trials. Difference in force between self- and external lifting trials giving rise to the same acceleration (horizontal line) can be taken as a measure of size of anticipatory response. *B*: average size of anticipatory response as a function of whether trial occurred before or after sustained trial. Unless otherwise stated, error bars represent SE across participants.

PERCEPTUAL JUDGMENTS. Participants correctly judged that there was no sustained force on unloading trials and rarely responded "no force" on sustained trials (0.54%). Psychometric functions were constructed for the remaining sustained trials, indicating the proportion of trials in which participants reported a force increase for each level of force change (Fig. 5*A*). Participants were more likely to report force increases on self-lifting trials compared with external lifting trials. For the unsupported trials, the average point of subjective equality (PSE; Fig. 5*B*) was 17.6 ± 4.4% lower for self-lifting and than for external lifting. Thus when a sensorimotor prediction is present, a 17% reduction in the sustained force applied to the postural hand was needed for the participants to judge that the force did not change from that perceived before unloading.

Interestingly, this illusion was not influenced by the anticipatory response itself or by motor errors. For the supported trials, the illusion was unchanged in size, with a difference in PSE of −23.5 ± 6.4% between self-lifting and external lifting. In a 2 × 2 ANOVA of the PSEs, the effect of self- versus external lifting was highly significant [$F(1,9) = 20.27$, $P < 0.001$], whereas the effect of support [$F(1,9) = 2.59$, $P = 0.142$] and the interaction [$F(1,9) = 0.95$, $P = 0.355$] were not significant.

Although the participants seemed to judge the force correctly in the external lifting trials, it is important to remember that the judgments were made relative to external trials as standards, thereby forcing the PSE in the external condition to zero. We will show in *experiment 2*, in which the absolute PSE could be interpreted, that the external lifting trials were also somewhat biased.

We asked whether the trial-by-trial variations in the sensorimotor prediction influenced the perceptual judgments. In Fig. 5*C*, we split the judgments in the unsupported self-lifting condition by the fitted sensorimotor prediction (z_n). As can be seen, the illusion became larger when the expected change was closer to the natural change of −100%.

In the supported and external lifting conditions, there was no anticipatory response, and we therefore could not fit the model to infer the sensorimotor prediction. However, we reasoned that, if the sensorimotor prediction was adapted in these conditions, this should occur in a similar way as in the unsupported self-lifting condition. We therefore used the parameters *A* and *B* from the unsupported self-lifting condition to infer the sensorimotor prediction on each trial, $z_1, \ldots, z_N$, in the other three conditions. The sensorimotor prediction was then entered for each of the four conditions as a continuous variable in a logistic regression (see METHODS) to model the force judgments. The estimated regression coefficients indicate how much the sensorimotor prediction influenced the perceptual judgment in each condition (Fig. 5*D*). The strongest influence was measured in the self-lifting, unsupported condition, with the mean of the regression weights being significantly smaller than zero [$t(9) = -2.69$, $P = 0.025$]. For the self-lifting, supported condition, the influence was slightly weaker, but still significant [$t(9) = -2.49$, $P = 0.034$]. A direct comparison of the two self-lifting conditions indicated no significant difference [$t(9) = 1.37$, $P = 0.203$]. For the two external conditions, the estimated sensorimotor prediction did not influence the perceptual judgments in either the unsupported [$t(9) = -1.64$, $P = 0.139$] or supported [$t(9) = 0.36$, $P = 0.73$] conditions. Thus in the self-lifting condition, the sensorimotor prediction seems to adapt on a trial-by-trial basis even in the absence of motor errors, and this rapid adaptation significantly influences the perception of force.

To summarize, the results of *experiment 1* show that the perception of force is closely linked to a sensorimotor prediction of the change in force. After self-lifting, the force remaining on the postural hand is perceived to be greater than that

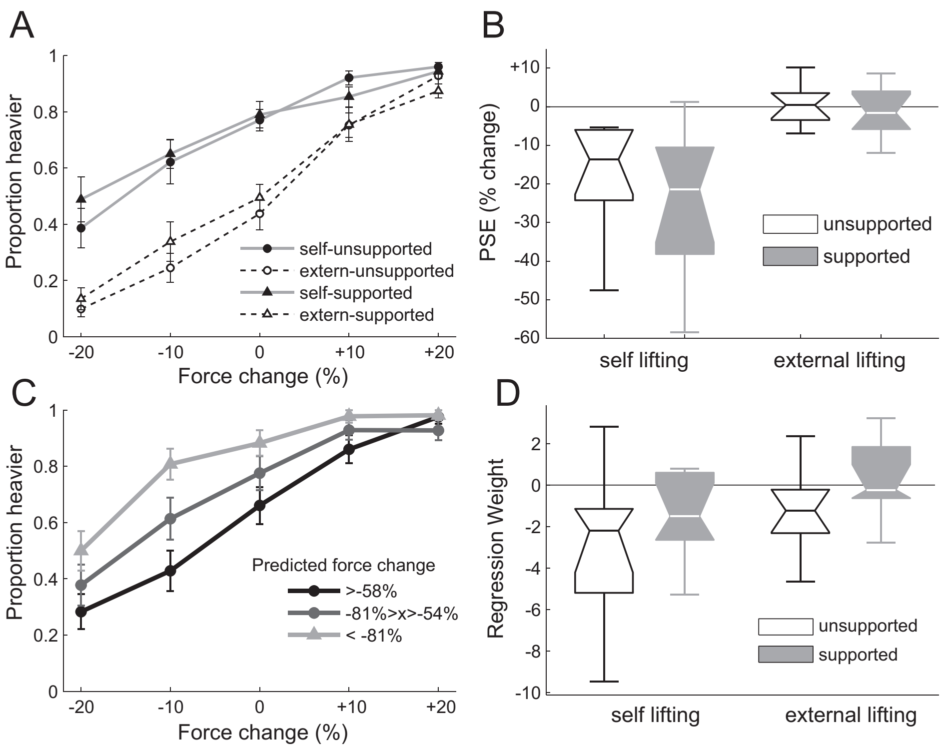

FIG. 5. Force judgments in *experiment 1*. *A:* proportion of heavier judgments is greater during self-lifting than during external lifting trials, with no difference between supported and unsupported trials. *B*: boxplot of point of subject equality (PSE)—force change necessary to be perceived as no change in force. Note that judgments were made relative to force change in external lifting trials. Horizontal lines indicate median, boxes indicate range of middle 50%, and whiskers indicate full range of PSEs of individual participants. *C:* judgment in unsupported self-lifting condition was influenced by history of force changes. As predicted force change approached force change that would occur under natural conditions (−100%), size of illusion increased. *D*: size of regression coefficient for predicted force change. More negative values indicate a stronger influence of predicted force change on perceptual judgment.

experienced after external lifting. Moreover, the persistent force is influenced by the trial-by-trial variation of the sensorimotor prediction. However, the actual occurrence of motor errors does not contribute to the illusion. We did not observe any differences in the magnitude of the illusion between the supported and unsupported trials.

There exist some other differences between the self- and external lifting conditions that could account for the differences in perception of force. First, the difference in perceptual judgments might be related to unloading speed given that the time of unloading was slightly delayed during self-lifting compared with external lifting. We conducted a secondary analysis restricted to the fastest half of the self-unloading trials. Here, unloading time was similar to that observed in the external lifting condition. With this partial data set, the difference in perceptual judgments between self- and external lifting conditions remained.

Second, the timing of the force change was predictable during self-lifting but not during external lifting. Third, in the self-lifting condition, participants felt a force with the lifting hand as they picked up the object; no forces were applied to the nonpostural hand in the external lifting condition. Although participants were explicitly instructed to make their judgments solely by considering the force on the postural hand, the presence of the other force may have biased their responses. In *experiment 2*, we address these latter two concerns and assess the influence of visual object information on the illusion.

Experiment 2

Studies of other illusions of perceived force such as the size-weight illusion (Flanagan and Beltzner 2000) have shown that visual object information can play a significant role in the final perception, independent of sensori-motor predictions. In *experiment 1*, participants saw an object leaving the postural hand in both the self- and external lifting condition. The visual information (e.g., not being able to attribute the force to an object) should therefore have influenced force judgments equally in both conditions. Because the judgments in *experiment 1* were made relative to the reference of external-lifting trials, this influence would not have been evident in *experiment 1*.

We therefore tested directly whether visual information about the object can influence the perception of force in *experiment 2*. Here we only tested sustained trials. This should quickly attenuate the sensorimotor prediction (and consequently the anticipatory response). We also manipulated the visual information directly by comparing two visual scenarios. The one-object condition was identical to *experiment 1*; an object, either self- or externally lifted, was seen to leave the hand (Fig. 1, *A–C*). In the two-object condition, one object remained on the postural hand and a second object was raised upward during lifting (Fig. 1, *D–F*).

ANTICIPATORY POSTURAL RESPONSE. The kinematic results for the postural hand were similar in the one- and two-object conditions; thus only the combined results are shown. The initial force change was slightly slower in the external than in the self-lifting condition (Fig. 6*A*). Because we excluded natural unloading trials, the anticipatory response during self-lifting was quickly extinguished, resulting in similar velocity

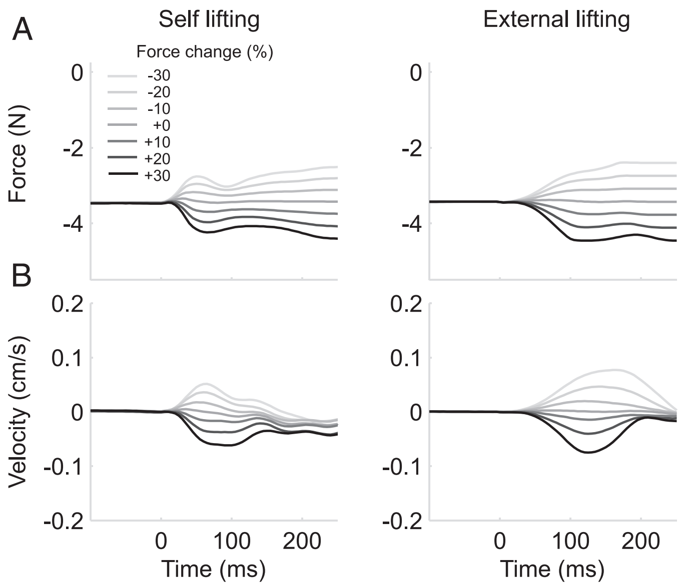

FIG. 6. *A*: average force, across participants and hands, on the postural hand in *experiment 2*. Unloading is faster in the self-lifting condition. *B*: average velocity profiles of postural hand are symmetric in both self- and external lifting conditions, indicating absence of an anticipatory response. Data are combined for 1- and 2-object conditions because results were similar.

profiles for self- and external lifting trials (Fig. 6*B*). In particular, the direction of the hand velocity reverses as a function of whether the sustained force was increased or decreased during self-lifting, as well as during external lifting. Thus no anticipatory response was present in the self-lifting trials.

PERCEPTUAL JUDGMENTS. In the one-object condition, the psychometric functions for the force judgments overlapped for self- and external lifting (Fig. 7*A*), resulting in nearly identical PSEs [$t(11) = -0.014$, $P = 0.98$]. This finding provides additional support for the hypothesis that the difference between self- and external lifting trials in *experiment 1* was caused by sensorimotor predictions. Other differences between the conditions, such as the predictability of the time of the force change or the force on the lifting hand, were the same in this experiment as in *experiment 1*. By eliminating the sensorimotor prediction through the use of sustained trials only, the difference between the self- and external lifting conditions was abolished.

We found, however, a significant difference in the PSE (Fig. 7*B*) between the one-object and the two-object condition [$F(1,22) = 24.93$, $P < 0.001$]. The mean PSE for the one-object condition, both for self- and external lifting, was -10%, significantly different from zero [$t(11) = -7.58$, $P < 0.001$]. Although the mean PSE for the external lifting condition in *experiment 1* was close to zero, it should be kept in mind that the judgments in *experiment 1* were made relative to external lifting trials as a standard, therefore clamping the external condition artificially to zero. In *experiment 2*, the absolute PSE can be interpreted, showing that visual information regarding the object alone can lead to a 10% shift in force judgment.

For the two-object condition, the PSE was -1.5%, a value that was not significantly different from zero [$t(11) = -1.45$, $P = 0.174$]. Therefore participants perceived an increase in force only when the virtual environment created a violation of a expectation; otherwise their judgment was unbiased. The size

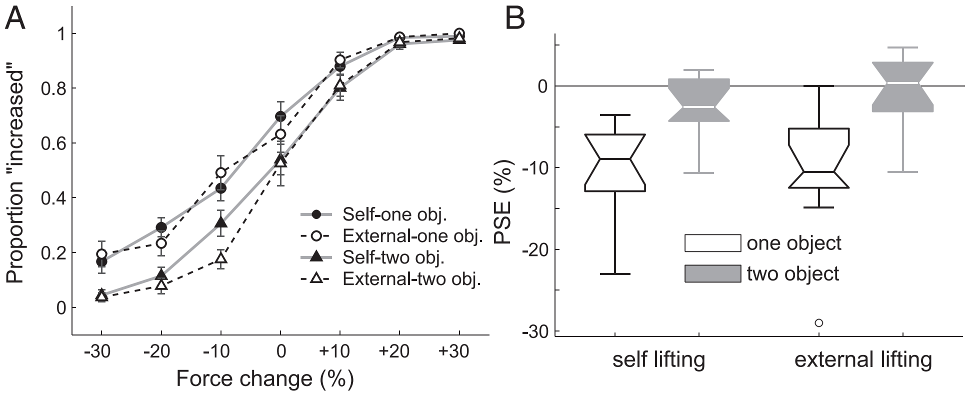

FIG. 7. *A*: proportion of increased force responses as a function of actual force change in *experiment 2*. *B*: point of subjective equality in the self-and external lifting conditions. Results indicate illusion in 1-object, but not 2-object, condition.

of this illusion induced by visual information was one half the size of the difference between self- and external lifting trials in *experiment 1*, which was induced by a violation of a sensorimotor prediction.

DISCUSSION

We report a novel force illusion, in which a constant force acting on a hand is perceived to increase when the apparent reason for that force is removed. This illusion arises because of a violation of an internal prediction. When an object is removed from a supporting hand, we expect that the load force generated by the object will be eliminated. The virtual reality environment allowed us to (serendipitously) observe this illusion by creating a somatosensory experience at odds with this expectation. The load force remained constant on the postural hand and participants perceived an increase in this force.

We sought to evaluate the role of three mechanisms that might underlie this illusion. In *experiment 1,* we found that the perception of the force depended on whether the load was lifted by a volitional action generated by the participant or by an external agent. The magnitude of this effect was substantial, with the illusion increased by ~20% during self-lifting. This result is congruent with previous work comparing self- and externally produced sensory stimuli (Bays et al. 2005; Blakemore et al. 1999; Shergill et al. 2003; Weiskrantz et al. 1971), and this difference is assumed to reflect the operation of sensorimotor predictions. A copy of the outgoing motor command, the efference copy (Von Holst 1954), is used to generate a sensorimotor prediction through a forward model of the motor system (Miall and Wolpert 1996; Wolpert et al. 1995). Thus sensorimotor predictions are closely linked to self-generated actions.

A novel finding in this study is that both the postural response and the force percept adapted on a trial-by-trial basis in a parallel manner. Similar to previous findings (Diedrichsen et al. 2005b), we found that anticipatory postural responses were significantly attenuated after a sustained trial. A similar adaptation was also found in the perceptual judgments. Interestingly, this adaptation occurred even when the postural hand was supported, eliminating any overt anticipatory postural response. Although our study provides no conclusive evidence, the finding of parallel trial-by-trial adaptation in action and perception is certainly in agreement with the hypothesis that both are caused by the adaptation of one common forward model (see Fig. 2) that is used to predict the sensory result of self-generated actions.

In contrast, we found very little evidence that the occurrence of motor errors, the downward perturbation of the postural hand, had any effect on the perception of the sustained force. This motor error dramatically alters the proprioceptive feedback from the arm; however, when we prevented these motor errors by having the arm rest on a rigid surface, the size of the illusion was unchanged. Although other studies have shown that illusions of force can arise under similar supported conditions (i.e., when motor errors are likely minimized, see Bays et al. 2005, 2006; Shergill et al. 2003), our experiment allowed us to assess the influence of motor errors directly. Surprisingly, we found that there was no influence. From this, we conclude that the perceptual illusion arises solely from the internal comparison of predicted and sensed sensory information rather than the perception of the hand's perturbation. This result also provides indirect evidence that, if the hand is perturbed downward, the nervous system correctly ascribes the perturbation to the changed postural motor command rather than to a further increase in load force. Thus the brain accurately accounts for the consequences of its own motor actions.

A central question in studies of motor learning concerns the types of error signals that are used to develop and modify sensorimotor predictions (Diedrichsen et al. 2005a). The error signal for this adaptation process could be sensory prediction errors, the difference between predicted and perceived sensory outcome, or motor errors, differences between the desired and actual movement of the limb (i.e., performance vs. prediction error, Jordan and Rumelhart 1992). This study provides evidence that prediction errors are sufficient for modifying sensorimotor predictions. The perceived force depended on the history of force changes in both the unsupported and supported conditions.

We found that contextual visual information about the external objects provided a second, independent mechanism that influenced the force illusion in this task. Participants perceived the sustained force to be ~10% larger when they saw the object being removed from the hand in the one-object condition compared with when one object remained on the hand in the two-object condition. Because of the delay in the visual system, the visual information about the displacement of the object from the hand in the external condition is only available after the force change on the postural hand is perceived. Nonetheless, the magnitude of the illusion was similar in the external and self-lifting conditions, even though the participant could generate a prediction of the forthcoming (visual) displacement in the latter condition. This suggests that, in contrast to sensorimotor predictions, the effect of visual context information on the perception of force in this experiment is postdictive rather than predictive (Bays et al. 2006). It is likely that the effects of visual information found in this study are similar to those found to mediate the size-weight and material-weight illusions (Ellis and Lederman 1998; Flanagan and Beltzner 2000).

Why do expectations influence our perception? Such a mechanism may be advantageous for two reasons. First, it attenuates the neural response to expected stimuli and, as such, helps amplify potentially important, unexpected sensory signals. Second, the bandwidth of firing rates in the nervous system is limited. Despite this, we can judge the weights of both very light and very heavy objects. By subtracting the expected value from the raw sensory percept, the dynamic range of a sensory channel can span a large interval of stimuli (Ross 1969). This comes at a price: the observer is no longer able to accurately judge the absolute value of a force stimulus.

In conclusion, our results provide clear evidence for a tight linkage between sensorimotor predictions and perception, whereby sensorimotor predictions directly influence perceptual processes (Fig. 2*B*). The indirect route, through the occurrence of motor errors (Fig. 2*C*), seems to have little influence on the percept, indicating that the nervous system correctly accounts for its own motor commands. We also showed that contextual, visual information of the workspace, even in the absence of a miscalibrated forward model, can influence force perception. This second mechanism, however, seems to act in a postdictive rather than predictive fashion.

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REFERENCES

Bays PM, Flanagan JR, Wolpert DM. Attenuation of self-generated tactile sensations is predictive, not postdictive. *PLoS Biol* 4: e28, 2006.

Bays PM, Wolpert DM, Flanagan JR. Perception of the consequences of self-action is temporally tuned and event driven. *Curr Biol* 15: 1125–1128, 2005.

Blakemore SJ, Frith CD, Wolpert DM. Spatio-temporal prediction modulates the perception of self-produced stimuli. *J Cogn Neurosci* 11: 551–559, 1999.

Blakemore SJ, Goodbody SJ, Wolpert DM. Predicting the consequences of our own actions: the role of sensorimotor context estimation. *J Neurosci* 18: 7511–7518, 1998.

Charpentier A. Analyse experimentale de quelques elements de la sensation de poids. *Arch Physiol Normal Pathol* 3: 122–135, 1891.

Diedrichsen J, Hashambhoy YL, Rane T, Shadmehr R. Neural correlates of reach errors. *J Neurosci* 25: 9919–9931, 2005a.

Diedrichsen J, Verstynen T, Hon A, Lehman SL, Ivry RB. Anticipatory adjustments in the unloading task: is an efference copy necessary for learning. *Exp Brain Res* 148: 272–276, 2003.

Diedrichsen J, Verstynen T, Lehman SL, Ivry RB. Cerebellar involvement in anticipating the consequences of self-produced actions during bimanual movements. *J Neurophysiol* 93: 801–812, 2005b.

Donchin O, Francis JT, Shadmehr R. Quantifying generalization from trial-by-trial behavior of adaptive systems that learn with basis functions: theory and experiments in human motor control. *J Neurosci* 23: 9032–9045, 2003.

Ellis RR, Lederman SJ. The golf-ball illusion: evidence for top-down processing in weight perception. *Perception* 27: 193–201, 1998.

Flanagan JR, Beltzner MA. Independence of perceptual and sensorimotor predictions in the size-weight illusion. *Nat Neurosci* 3: 737–741, 2000.

Haggard P, Clark S, Kalogeras J. Voluntary action and conscious awareness. *Nat Neurosci* 5: 382–385, 2002.

Hugon M, Massion J, Wiesendanger M. Anticipatory postural changes induced by active unloading and comparison with passive unloading in man. *Pfluegers* 393: 292–296, 1982.

Jordan MI, Rumelhart DE. Forward models: supervised learing with a distal teacher. *Cogn Sci* 16: 307–354, 1992.

Miall RC, Wolpert DM. Forward models for physiological motor control. *Neural Networks* 9: 1265–1279, 1996.

Ross HE. When is a weight not illusory. *Q J Exp Psychol* 21: 346–355, 1969.

Shergill SS, Bays PM, Frith CD, Wolpert DM. Two eyes for an eye: the neuroscience of force escalation. *Science* 301: 187, 2003.

Von Holst E. Relations between the central nervous system and the peripheral organs. *Br J Anim Behav* 2: 89–94, 1954.

Weiskrantz L, Elliott J, Darlington C. Preliminary observations on tickling oneself. *Nature* 230: 598–599, 1971.

Wolpert DM, Ghahramani Z, Jordan MI. An internal model for sensorimotor integration. *Science* 269: 1880–1882, 1995.