Illusory force perception following a voluntary limb movement

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We present a novel illusion in which participants report constant forces on their hand as steadily increasing. Participants made discrete reaching movements perturbed by a lateral force that increased with the distance moved; when stationary at the end of the movement, a true constant force was perceived to increase. We tested perceived subjective equality by increasing or decreasing the force. The illusion was significantly stronger when the perturbation was applied during active movement. We conclude that the unusual context of moving against lateral spring forces results in participants failing to predict steady lateral forces at the end of their movement, and causes an illusion of increasing forces even after movement termination. This result further emphasizes the role of action prediction in sensory perception. *NeuroReport* 21:675–679 © 2010 Wolters Kluwer Health | Lippincott Williams & Wilkins.

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Introduction

When we make a reaching movement, it is important that our hand gets to the right destination. To accomplish this, the motor system uses a combination of feed-forward prediction and visual/proprioceptive feedback [1–3]. Movement planning takes account of the context of the movement [4–6] to specify the initial feed-forward motor commands to the limb [2]. Visual and proprioceptive feedback from the ongoing action is used to correct for perturbations in limb trajectory [7,8].

It is unclear how the motor system behaves in a novel context, when it has no experience of a particular set of sensory consequences given a certain set of motor commands. Many studies have been carried out on reaching in both the stable and unstable force fields [9–12], but these reaching studies generally involve adapting to contexts that the motor system is used to handling. A completely novel context is rare, and as such it is assumed that the motor system would be unable to accurately predict the sensory consequences of an action in this case.

Here we report investigations into a newly discovered sensory illusion that takes place in such a novel context. Participants made a movement in a position-dependent field in which an increasing force was applied to their arm perpendicular to their movement direction. At the end of the movement, they had to stabilize their arm against a maintained constant force level. Under these conditions we found a surprising perceptual illusion: the force on the limb at the end of the movement appeared to increase over the course of a few seconds, but crucially the illusion only seemed to appear after a brisk reaching movement.

To quantify this illusion using the principle of perceptual constancy, we imposed a force ramp (gradient) at the end of each reaching movement that increased or decreased over time. From this we constructed a psychophysical function using a two-alternative forced choice paradigm to find force ramps that would cancel the participants' impression of an increasing force. We hypothesized from our pilot data that we would see a bias toward participants reporting static forces as 'increasing,' thus shifting the psychophysical function. We also included another condition designed to test whether it was the active movement that was important or just the impact of the force on a stationary arm. We also hypothesized that the illusion was at least partly because of the unfamiliar context of a lateral force impacting on a forward-reaching movement and thus, we conducted a follow-up experiment that aimed to explore the effect of force and target direction on its presentation.

Materials and methods
Participants

Ten participants took part in the experimental condition (3 male, 7 female, age range 19–37 years, median age 25.1 years, one left-handed) and 10 different participants took part in the control condition (all female, age range 18–31 years, median age 22.7 years, two left-handed). Thirteen more participants took part in the follow-up experiment (8 male, 5 female, age range 19–50 years, median age 29 years, four left-handed). All gave their informed consent.

None of the participants had any known motor or sensory abnormalities, and all were normal healthy adults with normal or corrected-to-normal vision. The experiment was approved by the local ethics committee at the University of Birmingham.

Apparatus and materials

The participants made reaching movements using their right hand on a vBOT robotic manipulandum [13]. They viewed a 0.5-cm red circular cursor showing the position of their hand using a projection-mirror system so that the cursor appeared to be in the same plane as their hand. Responses were gathered using the right foot on a pair of foot pedals.
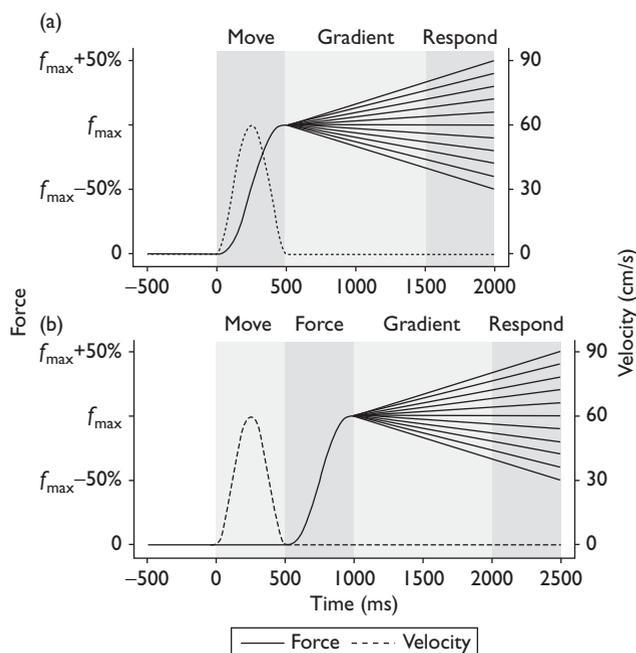
Procedure

In the movement condition (Fig. 1a), the participants moved the red cursor to a white starting circle at the bottom of the screen at the start of each trial. After 500 ms a blue target appeared 16 cm in front of the white starting circle and the participants were instructed to move to the target within 500 ms. If they did so the target turned yellow, otherwise it turned red (movement too quick) or green (movement too slow). Along the way

Fig. 1

(a)

(b)

Experimental procedure. (a) Schematic procedure for the movement condition showing the bell-shaped velocity profile of a typical forward-reaching movement, and the position-dependent lateral force imposed on the arm. At the end of the reaching movement, one of the 11 increasing or decreasing force ramps was applied. (b) Similar schematic procedure for static condition but showing that the force onset was after the movement completion.

to the target, the participants received a position-dependent force that pushed their arm to the right with a force constant of 0.72 N/cm measured along the axis from start to target, peaking at the target position at $f_{max} = 11.52$ N. The participants were required to counteract this force and stabilize their hand at the target. As soon as the target changed color, the participants experienced one of 11 force ramps over 1000 ms ranging from −50% (decreasing from 11.52 to 5.76 N) to +50% (increasing from 11.52 to 17.28 N) and including a 0% constant force. Force ramps were randomly interleaved from trial to trial. After 1000 ms, the target returned to its original blue color and the ramp continued while the participants had a further 500 ms to respond with the foot pedal as to whether the force was 'increasing' (toe) or 'decreasing' (heel). After this further 500 ms, if the participants had not made a response, the ramp was turned off and the trial was reshuffled into the remaining trials. Two hundred and twenty trials were carried out in total.

In the static condition (Fig. 1b), the participants moved to the white starting circle as in the movement condition. Another white circle then appeared 16 cm in front of the first one and the participants were instructed to move to this circle. There were no imposed forces during their movement. When they had reached it, the target turned blue and a rightward force that increased over 500 ms with a minimum jerk profile [14] was imposed on their static arm, again peaking at 11.52 N. The participants were again required to stabilize their hand at the target and resist this force. Immediately after the 500-ms force profile, the target turned yellow and the trial proceeded in the same way as in the movement condition with increasing or decreasing force ramps and a response by the participant.

In the follow-up experiment, the same protocol as the movement condition was followed except that the target could now be in one of the four directions (forward, backwards, left, and right with respect to the starting position; left and right flipped during analysis for left-handed participants) and the force could also act in one of these four directions. Thus, sometimes the force was assistive, sometimes resistive, and sometimes orthogonal to the movement direction. The participants performed 25 trials in each combination of target/force directions in a single block; as before, the gradients were randomized across the trials. The blocks were randomized and the participants were informed before each block what the target and force direction would be. Each participant received 400 trials in total.

Results

We hypothesized from pilot data that if the participants perceived an increasing force at the end of their movement even when the force was constant, then

(i) the psychometric function should be left shifted to reflect this bias and (ii) the number of 'increasing' responses at constant force should be significantly greater than chance. Figure 2 (solid line) shows the psychometric function formed from 'increasing' responses versus gradient, and this function is indeed left shifted. Furthermore, the mean percentage of 'increasing' responses at a constant force was 74.0% (SD: 13.9%), which was significantly greater than chance $[t(9) = 5.46, P < 0.001]$. We have used t-tests rather than d-prime values throughout, because at constant force the gradient was neither increasing nor decreasing, so there was no correct response.

We wondered whether the illusion shown in the movement condition was simply caused by an unexpected force on the hand rather than a consequence of the predictive movement system. To control for this possibility, we performed a static condition in which participants made similar judgements as before, but this time forces were only applied while their hand was still. Figure 2 (dashed line) shows the psychometric function plotting 'increasing' responses versus gradient in the static condition; the function is still left shifted, but less than in the movement condition. Furthermore, the mean percentage of 'increasing' responses at constant force was only 60.0% (SD: 14.5%), which was not significantly greater than chance $[t(9) = 2.18, P = 0.06]$, although there is a trend toward significance. However, a two-tailed, two-sample t-test on the percentage of 'increasing' responses at constant force across the two groups showed that the movement group responded 'increasing' sig-

nificantly more than the static group did $[t(18) = 2.20, P = 0.04$, Cohen's $d = 1.04]$ and thus, it seems clear that the illusion is stronger when moving through a novel movement-dependent force field than when an external force is applied to the static hand.

We were concerned that the participants might have had an underlying bias toward saying 'increasing' rather than 'decreasing,' as in the movement condition the participants correctly identified the largest positive gradient as 'increasing' 90% of the time (91% in the static condition) but reported the largest negative gradient as 'decreasing' only 78.5% (77.5%) of the time. The fact that the force increased as the participants moved may have caused this disparity. To correct for it, we shifted the entire curve down until the percentages of correct responses at the extremes were equal. After this correction, the mean percentage of 'increasing' responses at constant force in the movement condition was reduced from 74.0 to 68.3% (SD: 17.8%), but was still significantly greater than chance $[t(9) = 3.24, P = 0.01]$. In the static condition, the correction reduced the mean percentage of 'increasing' responses at constant to 53.0% (SD: 9.1%), which was still not significantly greater than chance $[t(9) = 1.04, P = 0.33]$. A two-tailed, two-sample t-test between the two groups still showed a difference $[t(18) = 2.41, P = 0.02$, Cohen's $d = 1.14]$.

Discussion
In the experiments presented here, we found that the participants experienced a perceptual illusion of increasing force when they moved their arm rapidly to a target in the presence of a laterally perturbing force field. The illusion was absent or much reduced when the force was presented after the movement rather than concurrent with it.

What is the source of these kinds of perceptual illusions? Although visual illusions are well known (for example see Ref. [15]) it is less common to find illusions in other sensory systems, perhaps because vision is our dominant sense. One recent example of an illusory force, which is similar to our illusion, comes from Diedrichsen *et al.* [16]. In their study, the participants supported an object with one hand and lifted it with the other. When the participants were presented with a force on their supporting hand, ostensibly from the object but that persisted after lifting, they reported that the force was perceived to be increasing when in reality it was constant. The investigators showed that prediction errors and visual information both contributed to the maintenance of the illusion. We cannot entirely rule out an effect of vision in our experiment. Opposing the lateral forces to maintain the cursor on target implies that the participants used visual guidance even after movement completion. However, preliminary data, not reported here, show that the illusion is also present in the absence of vision.

Fig. 2
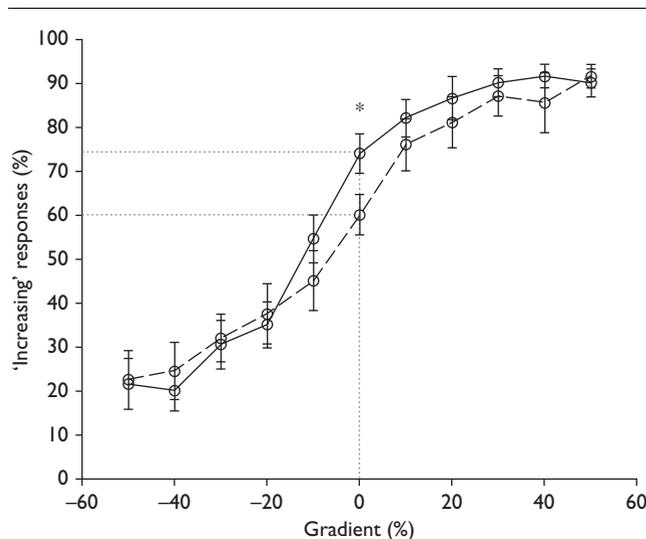
Psychophysical response functions from movement (solid line) and static (dashed line) conditions showing the percentage of 'increasing' responses against each force gradient. Note the significant difference (*) between movement and static at constant force. Each point in the group mean ± 1 SEM.

As in their study, it seems likely that requiring the participants to oppose a novel, movement-related force was the primary cause of the effect. When we move our arms, we are usually able to predict the sensory consequences of our action extremely well, as we have had lifelong experience in this particular arena. However, when these predictions are erroneous (in this case when the external force on the arm is applied in an unusual direction, atypical of normal object interactions) this mismatch between prediction and feedback might cause an illusory sensation. Note, however, that our illusion differs from the one described by Diedrichsen *et al.* [16] in that it has its effect on a single hand only.

Furthermore, our results from the static condition suggest that an important factor causing the illusion is reaching in the unusual force field. When participants made an unperturbed movement, stopped, and then had the force impact on their hand the illusion was much reduced; it only appeared consistently when the force impacted during the movement. This important difference is further evidence for the role of action prediction in the illusion, specifically the prediction of the consequences of the action from the efference copy of the motor command [3,17]. Presumably, the reduction of the illusion in the static condition occurs because the prediction that the arm will come to a halt with zero external force is fulfilled. When the force impacts on the stationary arm, the participant is now performing a postural stability task and the force is perceived to be an external event unrelated to the earlier actions. Another possible explanation is that sensory attenuation, known to occur during active movement (e.g. [18]), is gradually reduced after the reach, leading to the false percept of increasing force.

One interesting point is the atypical relationship between movement direction and imposed force, which tends to deviate the arm from its intended trajectory. We predicted that the illusion would therefore be greatest when forces were orthogonal to movement direction. Preliminary results from a follow-up study that tests the presence of the illusion in different movement orientations and for different force directions indicate that the illusion is strongest when the force on the limb pushes it to the left or right with respect to the trunk, rather than forward or backward. When we reach an unstable environment, the motor system must selectively control the impedance geometry – that is, the stiffness of the limb – to stabilize the arm [19]. Although the participants tend to increase their stiffness depending on the direction of instability in the environment [20], there is an inherent variation in stiffness in the neuromuscular system across different arm orientations. Our result, shown in Table 1, supports the idea that the illusion is affected by the inherent stability of the limb, perhaps because we are able to deal with perturbations in the

forward/backward axis more easily than the left/right direction.

Table 1 Percentage of 'increasing' responses at constant force during movements and force perturbations applied in four directions

	Forward (%)	Backward (%)	Left (%)	Right (%)
Force direction	54.2	56.9	65.0**	66.2***
Target direction	61.2**	59.6*	58.1*	63.5**

The illusion was apparent in all target directions and when the force was applied in the left and right directions, but not forward and backward directions. The 4 × 4 analysis of variance of force by target direction showed a main effect of force direction [F(3,192) = 2.85, P = 0.039] but no effect of target direction and no interaction. Statistics in the table are based on uncorrected *t*-tests between the percentage of 'increasing' responses for each force and target direction versus chance (50%).
*P < 0.05.
**P < 0.01.
***P < 0.001.

Conclusion
In conclusion, we have shown the existence of a novel force illusion that presents as the apparent increase in perceived force at the end of a movement when, in fact, the force on the limb is constant. Our identification of a perceptual sensory illusion operating within a single limb, and that is apparently not dependent on visuomotor discrepancies, is therefore novel. The illusion does not seem to be as strong when the force impacts on the stationary limb, and may be because of the mismatch between the predicted and actual outcome of voluntary movement, or the reduction of sensory attenuation after a movement. Our hypothesis that the illusion is strongest when the force perturbation is applied orthogonal to the movement direction (which is unusual in everyday experience) was only partly supported, and instead, there is evidence – albeit weak – that the illusion may be modulated by the anisotropic stiffness of the arm in different reaching movements.

Acknowledgement

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