

# A New Look at Sensory Attenuation: Action-Effect Anticipation Affects Sensitivity, Not Response Bias

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Psychological Science  
 21(12) 1740–1745  
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 DOI: 10.1177/0956797610389187  
<http://pss.sagepub.com>  


## Abstract

The systematic association of an action that a person performs with its sensory effects is thought to attenuate that person's perception of the effect of the action. However, whether learned sensorimotor contingencies truly affect perception, rather than just inducing a response bias, has yet to be determined. The experiment presented in this article comprised two parts: an action-effect association phase and a test phase, during which the actions' perceptual effects were tested. During the association phase, specific actions (left-key and right-key presses) were associated with specific visual effects (tilted Gabor patches). In the test phase, participants' left-key presses and right-key presses triggered the onset of a low-contrast tilted Gabor patch in 50% of trials (no stimulus was presented on the remaining 50% of trials). Participants were required to report the presence or absence of this tilted Gabor patch. Our results showed that participants' sensitivity ( $d'$ ) to the Gabor patches was reduced by 10% when the patches were triggered by the action they had previously been associated with. This finding indicates that a person's action does not induce a response bias ( $c$ ), but changes the perception ( $d'$ ) of the learned action effect.

## Keywords

sensorimotor contingency, sensory suppression, signal detection theory

Received 9/22/09; Revision accepted 5/12/10

The human brain uses body movements (e.g., Wexler, Panerai, Lamouret, & Droulez, 2001) and voluntary actions to interpret sensory changes (e.g., Pelah & Barlow, 2001). Voluntary actions are thought to involve internal forward models that predict the sensory consequences of each action (e.g., Wolpert & Ghahramani, 2000; Linser & Goschke, 2007). The prediction of the sensory consequences of actions can potentially enhance humans' abilities to detect changes in the environment and differentiate these changes from ones brought about by the individuals themselves (e.g., Cullen, 2004). This theory of internal forward models is supported by findings that manual movements result in the sensory attenuation of predicted effects of the movements. It is likely that an individual can predict sensation for a given action and compare the predicted sensation with actual feedback: If the two match, the anticipated sensations are canceled (e.g., Wolpert, 1997). This could explain, for example, why it is difficult to tickle oneself (Blakemore, Wolpert, & Frith, 2000).

In our study, we tested whether internal action-effect anticipation genuinely alters the perception of the effect of the

action, or whether it merely induces a response bias. According to signal detection theory (Green & Swets, 1966), a sensory process transforms a stimulus into an internal response (or representation), and a decision process enables an individual to determine on each trial whether or not the stimulus is present, given the current value of the internal response and the decision criterion. The difference between the mean and standard deviation of the distributions of internal responses elicited in trials in which the stimulus is physically present (signal distribution) in comparison with the mean and standard deviation of responses elicited in trials in which it is absent (noise distribution) characterizes sensitivity ( $d'$ ). The higher the  $d'$  value is, the more effectively the perceptual system differentiates signal from noise. The decision or response criterion ( $c$ ) is the value that indicates the level that an internal

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response has to exceed for the participant to report that the stimulus is present. The lower the  $c$  value is, the smaller the internal responses are that the perceptual system still accepts as indicating that a stimulus is present.

Usually, studies on sensory attenuation use the point of subjective equality or equivalent techniques (e.g., Haggard & Whitford, 2004; Sato, 2008; Tsakiris & Haggard, 2003). It is important to note that the percentage of correct responses is affected by both response criterion and sensitivity. This means that a given percentage of correct responses (e.g., 75%) can result from multiple combinations of criterion and sensitivity (e.g.,  $d' = 2, c = 2$  and  $d' = 3, c = 3$ ). The percentage of correct responses thus confounds sensitivity and response criterion. Consequently, studies on sensory attenuation that use the point of subjective equality or equivalent techniques cannot rule out that sensorimotor contingencies alter participants' response bias rather than their perception. The hypothesis that sensorimotor contingencies alter the response bias is plausible, as systematic action-effect associations necessarily affect the conditional probabilities of the stimuli, which are known to affect the criterion (e.g., Gorea & Sagi, 2000; Tanner, Swets, & Green, 1956; Waszak & Gorea, 2004). In the experiment we present in this article, by contrast, we used signal detection theory to measure subjects'  $d'$  and  $c$  values separately, and

hence to assess unequivocally the nature of sensory attenuation.

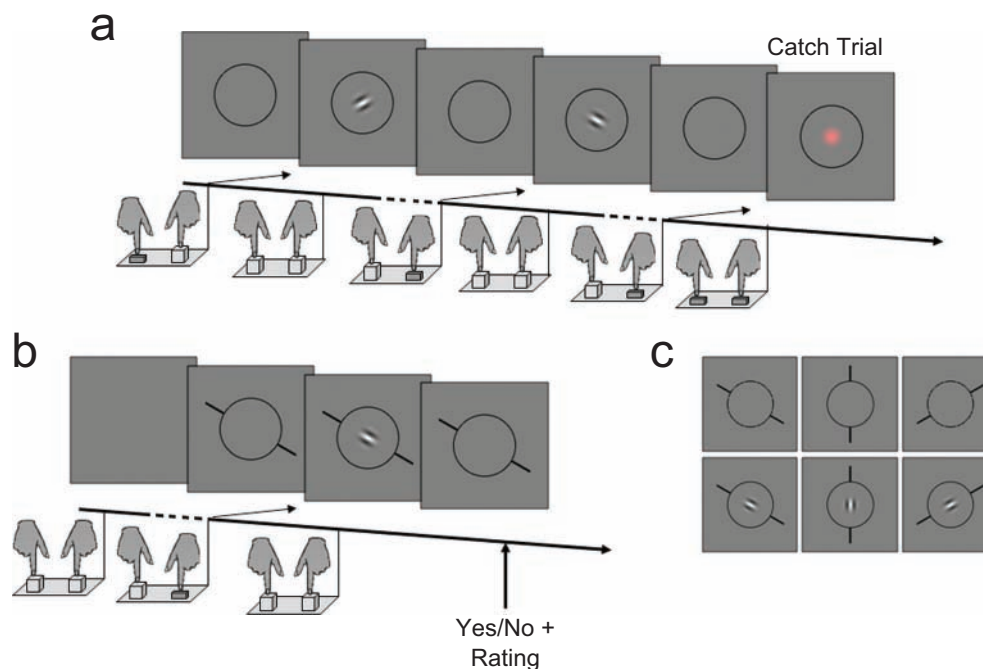
Stimuli were Gabor patches (spatial frequency of 4 cycles/deg; stimulus-size  $SD = 0.762^\circ$ ) presented in the center of a computer screen (19-in/ CRT;  $1024 \times 768$  pixels, 100-Hz refresh rate; background luminance =  $40 \text{ cd/m}^2$ ). The screen's center was highlighted by a circle ( $20 \text{ cd/m}^2$ , thickness of  $0.109^\circ$ , inner diameter of  $6.52^\circ$ ) that was constantly visible during stimulus presentation (see Fig. 1).

This study included a main experiment and a control experiment, each of which consisted of an acquisition phase (see Fig. 1a) and a test phase (see Fig. 1b). During the acquisition phase, an association was formed between a particular visual effect and either an action (main experiment) or a specific sound (control experiment). The test phase assessed the influence of this association on the perception of low-contrast visual stimuli.

## Main Experiment

### Method

**Acquisition phase.** Participants produced a random sequence of left-key and right-key presses (via the left and right arrow



**Fig. 1.** Experimental stimuli. The example trial from the association phase (a) illustrates that left-key presses and right-key presses were differentially associated with rightward-tilted Gabor patches and leftward-tilted Gabor patches. In catch trials, a red Gaussian blob was shown instead of a Gabor patch, and participants were required to press the left and right keys simultaneously. In the test phase (b), two line segments attached to the central circle cued an orientation and were presented during the entire trial. The participant's key presses triggered the onset of a low-contrast Gabor patch with the same orientation as the line segments at the screen's center on 50% of trials; no Gabor patch was displayed on the remaining 50%. Participants were asked to report whether or not they had seen a Gabor patch with the same orientation as the line segments and then to rate their confidence in their response. The illustration in (c) shows all the stimuli used in the test phase: Circles with line segments cuing the orientation of the Gabor patch to be detected (left, right, or vertical) were presented either with (bottom row) or without (top row) the Gabor signal.

keys on a keyboard, respectively) using the left and right index fingers, at a pace of about 0.5 key presses/s. Feedback confirming that the sequences were random was generated every 50 trials, followed by a short break. Each key press produced a visual stimulus that followed a Gaussian temporal profile, peaking at 50% luminance contrast at 200 ms ( $SD = 100$  ms) after the key press. For half of the participants, a right-key press produced a rightward-tilted ( $-60^\circ$  relative to vertical) Gabor patch, and a left-key press produced a leftward-tilted Gabor patch ( $+60^\circ$ ). For the other half of the participants, the reverse mapping was used (i.e. a right-key press produced a leftward-tilted Gabor patch, and a left-key press a rightward-tilted Gabor patch). In 5% of the trials, participants saw the onset of a red Gaussian blob in response to their key press and were required to immediately press both the left key and the right key at the same time. The acquisition phase of the experiment consisted of 450 trials and lasted for an average of 13.1 min ( $SEM = 0.309$  min).

**Test phase.** As in the acquisition phase, participants produced a random sequence of left-key and right-key presses and received feedback; the difference was that only half of the key presses produced a Gabor patch. In addition, these Gabor patches were presented at a contrast level that was individually determined in a preliminary experiment to produce a detection  $d'$  of 2 (mean contrast = 3.91%,  $SEM = 0.32\%$ ). Three orientations of the Gabor patches ( $-60^\circ$ ,  $0^\circ$ , or  $+60^\circ$ ) were presented in random order. On congruent trials, the participants' key press produced the Gabor patch that was associated with that same key press in the acquisition phase. Therefore, the learned and actual action effects were congruent. On incongruent trials, the key press produced the Gabor patch associated with the opposite hand in the acquisition phase. We included the  $0^\circ$  orientation as a neutral condition (i.e., this orientation was not previously associated with either the left hand or the right hand); this condition controlled for any effects on  $d'$  and  $c$  resulting from the presentation of the Gabor stimuli during the test phase (i.e., effects independent of the specific action the patches were associated with). Our study focuses on the difference between the congruent and incongruent conditions: The sensory-attenuation hypothesis predicts a lower  $d'$  in the congruent condition than in the incongruent condition.

It would have been impossible to interpret participants' performance in terms of sensitivity and response criterion if they had been asked to detect any stimulus rather than a specific stimulus, because participants' responses could not have been unequivocally allocated to one of the three orientations. To allow for measurement of sensitivity and criterion, we split the detection of the three different Gabor stimuli into three simple one-dimensional detection tasks, using orientation cues. Each cue consisted of two parallel line segments ( $2.18^\circ$  long,  $0.109^\circ$  thick) that were attached above and below the central circle, indicating the orientation of the Gabor patch for the duration of the trial.

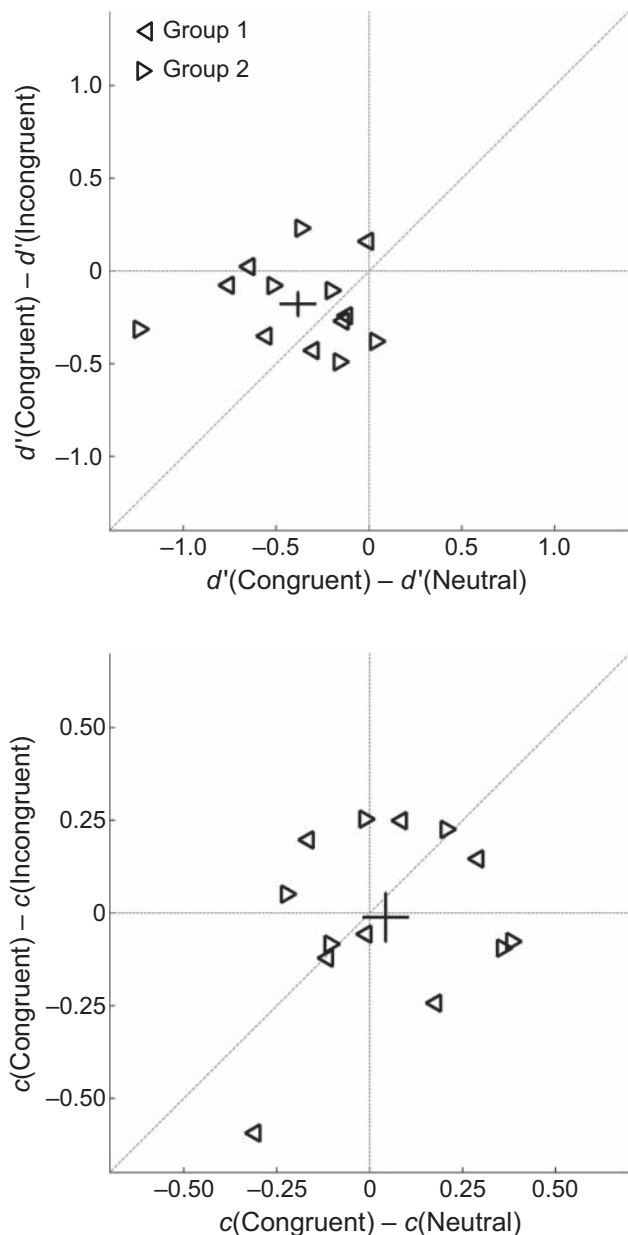
The orientation cues also minimized high-level expectation effects, as participants always knew which stimulus to expect.

Participants were informed that in 50% of the trials, their left-key or right-key press would produce a Gabor patch in the orientation defined by the orientation cue (i.e.  $-60^\circ$ ,  $0^\circ$ , or  $+60^\circ$ , randomly interleaved across trials), and that in the remaining 50% of the trials, the key press would produce no visual effect.<sup>1</sup> One second after a key press, the messages "yes" and "no" were presented alternately on the screen (600 ms/message). Participants pressed both keys to select the appropriate message, which remained on the screen. After this first response, the messages "low," "medium," and "high" were presented alternately below the previous response ("yes" or "no"). Participants pressed both keys to select the message indicating their level of confidence in their previous response. This procedure was used to avoid possible bias from a one-handed response being used both to report the decision and to trigger the next trial. The acquisition phase of the experiment consisted of 600 trials and lasted an average of 56.2 min ( $SEM = 2.93$  min).

**Participants.** Sixteen naive observers participated in the main experiment; 3 were excluded from the analysis as their sensitivity level was either too high (the stimulus was always correctly detected) or too low ( $d' = 0.441$ ; the remaining 13 participants had an average  $d'$  of 2.56,  $SEM = 0.175$ ). Of the remaining participants (7 women, 6 men; mean age = 24.8 years,  $SEM = 0.709$  years), 7 individuals belonged to Group 1, and 6 individuals belonged to Group 2. The two groups differed in the specific action-effect associations during the acquisition phase of the experiment. For Group 1, a left-key press was followed by a Gabor patch tilted to the left, and a right-key press was followed by a Gabor patch tilted to the right; for Group 2, the action-effect mapping was reversed.

## Results

To assess the effects of learned action-effect associations, we computed participants' sensitivity and response criterion separately for the three conditions (incongruent, neutral, and congruent):  $d' = z(\text{hit rate}) - z(\text{false alarm rate})$ ;  $c = -0.5 \times [z(\text{hit rate}) + z(\text{false alarm rate})]$ . The top panel of Figure 2 presents the  $d'$  difference between the congruent and incongruent conditions as a function of the  $d'$  difference between the congruent and the neutral conditions. For almost all subjects,  $d'$  was smaller in the congruent condition than in the neutral and incongruent conditions. A repeated measures analysis of variance (ANOVA) revealed a significant effect of condition on  $d'$  (incongruent:  $M = 2.55$ ,  $SEM = 0.191$ ; neutral:  $M = 2.75$ ,  $SEM = 0.183$ ; congruent:  $M = 2.37$ ,  $SEM = 0.174$ ),  $F(2, 24) = 7.96$ ,  $p = .0022$ . Furthermore, paired  $t$  tests showed no difference between the incongruent and neutral conditions,  $t(12) = -1.72$ ,  $p = .11$ , but a significant difference between the congruent and neutral conditions,  $t(12) = 3.87$ ,  $p = .0022$ , as well as between the congruent and incongruent conditions,  $t(12) = 2.86$ ,  $p = .0143$ . Hence, performing an action reduced sensitivity to the action effect by about 10% on average when the actual action effect corresponded to the effect associated with a particular action.



**Fig. 2.** Effect of the acquired action-effect association on visual sensitivity ( $d'$ ; top panel) and the decision criterion ( $c$ ; bottom panel) in the main experiment; the difference in  $d'$  or  $c$  between the congruent and incongruent conditions is presented as a function of the difference in  $d'$  or  $c$  between the congruent and neutral conditions. The central cross represents the population mean and standard error of the mean.

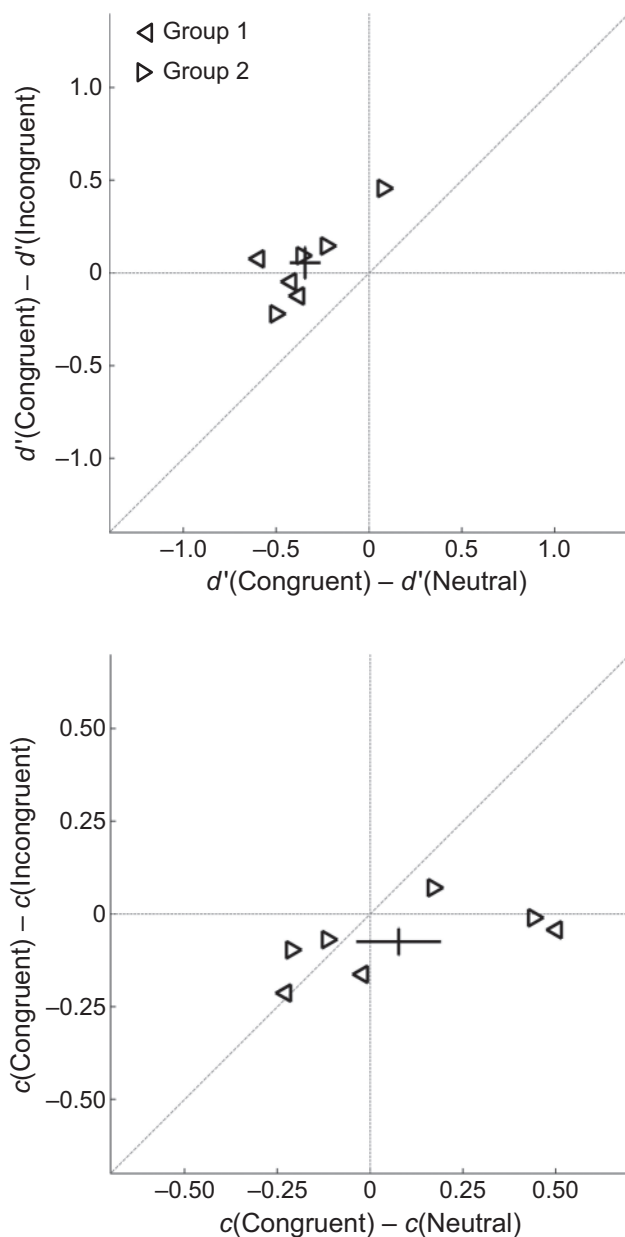
To check whether this reduction in  $d'$  was truly a sensitivity change, it was necessary to show that the response criterion ( $c$ ) did not differ between conditions (see Fig. 2, bottom panel). Indeed, if the assumption of equal signal and noise variances is not met, a change in criterion would lead to a change in  $d'$  even in the absence of a sensitivity difference (Green & Swets, 1966). A repeated measures ANOVA on the criteria failed to show any difference in  $c$  between conditions,  $F(2, 24) = 0.342$ ,  $p = .714$ .

To ensure that these results were not due to a specific action-effect mapping (e.g., a left-key press associated with a left-tilted Gabor), we performed a two-way repeated measures ANOVA on  $d'$  and  $c$ , with congruency (congruent, incongruent, or neutral) and mapping group (left key–left Gabor, right key–right Gabor or left key–right Gabor, right key–left Gabor) as factors. The Congruency  $\times$  Mapping Group interaction was not significant— $d'$ :  $F(2, 22) = 0.03$ ,  $p = .971$ ;  $c$ :  $F(2, 22) = 0.24$ ,  $p = .791$ . Hence, the observed sensitivity reduction could be instantiated by arbitrary action-effect associations.

## Control Experiment

Finally, to ascertain that the sensitivity reduction was due to internal action-effect anticipation rather than to learned statistical regularities between actions and effects, we ran a control experiment that was identical to the main experiment with the exception that the Gabor orientations were not differentially associated with left-key and right-key presses, but were instead differentially associated with high- and low-pitch tones: In the association phase, participants pressed both left and right keys for about 1 s, releasing them to trigger the onset of a left- or right-tilted Gabor (as in the main experiment). A high-pitch tone or a low-pitch tone was presented while the keys were pressed and predicted perfectly the orientation of the subsequent Gabor patch (as the key presses did in the main experiment). In the test phase, participants again pressed both keys. Releasing them triggered the test Gabor (on 50% of trials). In this phase, a high- or low-pitch tone was played randomly while the keys were pressed. Seven new naive observers (4 women, 3 men; mean age = 26.3 years,  $SEM = 1.25$  years) participated in this control experiment.

The results of this experiment are depicted in Figure 3. Congruent trials were the subset of trials in which the tone (high or low pitch) was presented with the Gabor orientation it had been coupled with in the association phase, incongruent trials were those in which the mapping of tone with Gabor orientation used in the association phase was reversed, and neutral trials were those in which the orientation had not previously been associated with a tone. Systematic audiovisual associations during the learning phase did not affect the response criterion,  $c$ . A repeated measures ANOVA on  $c$  revealed that condition did not have a significant main effect (incongruent:  $M = 0.628$ ,  $SEM = 0.322$ ; neutral:  $M = 0.477$ ,  $SEM = 0.277$ ; congruent:  $M = 0.554$ ,  $SEM = 0.323$ ),  $F(2, 12) = 1.475$ ,  $p = .268$ . A repeated measures ANOVA on  $d'$  yielded a main effect of condition,  $F(2, 12) = 17.171$ ,  $p = .0003$ ;  $d'$  values in the neutral condition ( $M = 2.262$ ,  $SEM = 0.571$ ) were significantly different from  $d'$  values in either the incongruent condition ( $M = 1.8626$ ,  $SEM = 0.594$ ),  $t(6) = 7.677$ ,  $p = .0003$ , or the congruent condition ( $M = 1.917$ ,  $SEM = 0.591$ ),  $t(6) = 4.194$ ,  $p = .0057$ . Thus, previous exposure to a stimulus affected its perception. Unlike in the first experiment, there was no  $d'$  difference between the congruent and incongruent conditions,  $t(6) = 0.654$ ,  $p = .538$ . This result shows that statistical regularities alone cannot explain



**Fig. 3.** Effect of the acquired action-effect association on visual sensitivity ( $d'$ ; top panel) and the decision criterion ( $c$ ; bottom panel) in the control experiment; the difference in  $d'$  or  $c$  between the congruent and incongruent conditions is presented as a function of the difference in  $d'$  or  $c$  between the congruent and neutral conditions. The central cross represents the population mean and standard error of the mean.

sensory attenuation (see also Richters & Eskew, 2009). However, it is still possible that cues more similar to key presses (e.g., tactile stimulation of the fingers) might be more likely to be associated to the Gabor stimuli.

## Discussion

In the acquisition phase, left-key presses and right-key presses produced tilted Gabor patches. In the subsequent test phase, participants' sensitivity to these Gabor patches was reduced by

about 10% when the patches were triggered by the key press they had previously been associated with. Our study thus demonstrates for the first time sensory attenuation that is based on learned arbitrary associations between (manual) movements and (visual) effects. It is important to note that we used signal detection theory in our analysis to assess both sensitivity ( $d'$ ) and response bias ( $c$ ), with  $d'$  representing the distribution of the internal response to the stimulus compared with the baseline (i.e., noise) distribution, and  $c$  representing the participant's tendency to privilege a particular decision outcome irrespective of the stimulus (see Green & Swets, 1966). All previous experiments have, to the best of our knowledge, used a methodology that confounds  $d'$  and  $c$ , making it impossible to determine the specific cause of observed performance changes. Our data demonstrate an effect of action-effect anticipation on perception ( $d'$ ), but not on response bias ( $c$ ).

We see three possible distinct accounts of this sensory attenuation. First, the central nervous system may predict the sensory consequences of an action and inhibit the relevant neurons, possibly to improve the detection of changes in the environment that are unrelated to the agent. In terms of signal detection theory, this inhibition account assumes that the mean of the signal distribution is decreased, thus making signal and noise less distinctive and  $d'$  smaller. This account relates to the notion that predicted effects are subtracted from the actual sensory effect at early processing stages, as assumed by the cancellation model (Sperry, 1950; von Holst & Mittelstaedt, 1950) to explain visual stability across eye movements (cf. Bays & Wolpert, 2007). Second, if a sensory effect is expected to occur after an action, fewer resources could be devoted to its encoding (resource-allocation account). In this case, sensory attenuation would not result from an attempt to cancel out self-action-related stimulations, but would rather be the consequence of resource optimization.

The third account of the observed sensory attenuation—the one we favor—is the preactivation account, which posits that the preparation or execution of an action preactivates sensory networks that represent the actions' expected perceptual consequence, thus increasing the mean level of activity to some pedestal level. The sensitivity loss observed for congruent action effects in this scenario is due to discrimination of the signal activation from the pedestal level being more difficult than discrimination of the signal activation from the baseline level (i.e., in the incongruent and the neutral conditions, in which baseline activity in the neurons coding the action effect is not raised to pedestal levels). In contrast to the inhibition account, in the preactivation account,  $d'$  in congruent trials is thought to be reduced not because the mean of the signal distribution is decreased, but rather because the mean of the noise distribution is increased. One way to conceptualize this noise-level increase is via ideomotor theory (cf. Harless, 1861; James, 1890; Lotze, 1852), which posits that performing an action results in a bidirectional association between the action and its sensory effects. Once acquired, these associations are used to select an action by internally activating their

perceptual consequences, such that performing an action involves the same representation as perceiving the effect it is associated with (e.g., Elsner & Hommel, 2001; Greenwald, 1970; Herwig, Prinz, & Waszak, 2007; Prinz, 1997; Waszak & Herwig, 2007; see also the common-coding theory, e.g., Hommel, Müsseler, Aschersleben, & Prinz, 2001; Prinz, 1990).

The results of our study show that the perception of visual action effects is impaired when the effects are triggered by an action that habitually produces these effects, and that this has a genuine effect on sensitivity. Further research in this field is needed to fully determine the mechanisms underlying internal action-effect anticipation.

### Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

### Funding

This study was funded by the Agence Nationale de la Recherche (ANR-08-FASHS-13) and the German Research Foundation (DFG; Schu2471/1-1). Pedro Cardoso-Leite was supported by the Fyssen Foundation.

### Note

1. The orientation of the cue presented did not bias participants' actions (i.e., the choice of which key to press on a given trial). Chi-square tests (Hand  $\times$  Orientation) revealed a significant bias for only 1 out of 16 participants,  $\chi^2(1, N = 16) = 5.38, p = .02$  (the average  $p$  value across participants was .369,  $SEM = .053$ ).

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