Embodiment of approach-avoidance behavior: Motivational priming of whole-body movements in a virtual world

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Abstract

Previous studies showed that humans can flexibly reconfigure manual reactions to motivational stimuli in order to produce compatible changes in visual environments (i.e., approach appetitive and avoid aversive stimuli). Using a virtual reality headset, we examined whether analogous flexibility is observed with whole-body movements in forward and backward directions that produced (non-)corresponding visual movements in a virtual environment. Two experiments showed that initiation of a forward movement was facilitated in response to a (pleasant) flower and a backward movement in response to an (unpleasant) spider, even when the movements resulted in reverse visual motions towards the spider and away from the flower. In contrast, visual motions were more important when attention was shifted to the visual motions in the virtual world (Experiment 3) or when these motions were controlled manually (Experiment 4). Overall, results suggest that there is a highly overlearned connection between locomotion and approach/avoidance that is difficult to override. A perceptual control theory of embodied motivated action is proposed.

Keywords: approach-avoidance; embodiment; 3D virtual reality; perceptual control systems;

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Humans and animals are predisposed to approach appetitive and to avoid aversive stimuli or end-states (Elliot, Eder, & Harmon-Jones, 2013). Previous studies suggested a tremendous flexibility in the control of approach-avoidance behaviors. For example, depending on the action context, humans can withdraw from aversive stimuli by either flexing or extending the arm (e.g., Bamford & Ward, 2008; Eder & Rothermund, 2008; Markman & Brendl, 2005; Wickens, 1938). This behavioral flexibility makes evolutionary sense because humans must cope with manifold threats and dangers in situations for which rigid motor patterns would often be inadequate (Caro, 2005). Consequently, modern theories have emphasized more the importance of goals, and less that of the motoric means, for the control of approach-avoidance behaviors (e.g., Eder & Hommel, 2013). To preempt the present results, this strong emphasis on behavioral flexibility is likely unwarranted: while movements of the hand can be flexibly reconfigured in the service of approach and avoidance goals, whole-body locomotion in forward/backward directions is more rigidly linked.

Evidence for flexible behavior control comes from computerized tasks in which symbolic approach/avoidance movements were dissociated from the producing manual actions (e.g., keypresses or lever movements). It was concluded that performance in these tasks was controlled by goals to move close to appetitive stimuli and away from aversive stimuli, while arm flexion/extension implementing these motions had no effect (for meta-analyses see Beatty, Cranley, Carnaby, & Janelle, 2016; Laham, Kashima, Dix, & Wheeler, 2015). Other studies investigated more complex movement chains in which a manikin (symbolizing the self) initially had to be moved in directions opposite to the intended end position. Results showed that such incongruent intermediate action steps had no systematic effect on approach-avoidance tendencies (Krieglmeyer, De Houwer, & Deutsch, 2011; Reichardt, 2018a, 2018b). This research suggests that behavioral performance in these tasks was controlled by the intended end-state, while the action path leading to this end-state was not important.

In contrast to these symbolic tasks, animal research revealed a rather rigid link between appetitive motivations and forward movement. In a classic study, Hershberger (1986) placed 4-day old chicks in a straight runaway containing a food cup from which they had been trained to eat. Importantly, the food cup (and the surrounding visual environment) always moved in the same direction in which the chick moved. For the experimental chicks, the cup moved twice as far as the chick itself; consequently, the distance to the food increased by walking towards it, and reduced only by walking away from it. For the controls, the cup moved half as far as the chick; they could thus reach the food bowl by running toward it. Results showed that the experimental chicks had substantial problems to reach the food cup. They showed only a small improvement despite an extended training period, irrespective of whether only the cup or the total environment including the cup was moved. It seemed that the hungry chicks were tuned by nature to approach food by running towards it.

To summarize, human and animal studies have used similar methods to examine the role of body movements in the pursuit of approach/avoidance goals, namely, to vary the mapping of body movements and (visual) movement consequences indicative of approach/avoidance. Yet, while human studies suggested a high degree of flexibility of linking body movements to such goals (Beatty et al., 2016; Laham et al., 2015), animal studies suggested a relatively hard-wired link between appetites and moving forward and threat processing and retreat, respectively (Bolles, 1970; Hershberger, 1986; for a modern review see Kim et al., 2017). Besides the obvious difference in the study subjects (humans *vs* animals), one explanation could be that animal research studied animal behavior in relatively naturalistic environments, whereas humans often acted symbolically in computerized tasks (e.g., moving a manikin around on the computer screen). It is plausible that the relevance of sensorimotor associations was downplayed by these artificial tasks (for evidence see Rougier et al., 2018). In addition, it can be hypothesized that whole-body movements in forward/backward directions are more closely linked to approach/avoidance motivations, respectively, due to their consistent mapping in the physical world.

In fact, several studies found that exposure to affective stimuli influences the initiation of locomotion. In one study, for example, participants were asked to walk toward pictures that appeared on a screen a few meters away (Naugle et al., 2011). Instructions were to initiate the walking movement as quickly as possible after picture offset, and initiation times of the first gait were analyzed as a function of picture valence (pleasant/unpleasant) and arousal (high/low). Results showed that exposure to high arousing unpleasant pictures speeded participants' reaction times compared to all other affective picture categories. Stins and Beek (2011) measured reaction times to initiate a forward or backward step from a bipedal stand and found, in contrast to the study Naugle and colleagues, that forward steps were initiated faster on the appearance of pleasant compared to unpleasant pictorial stimuli; however, no difference was observed in initiation times of backward steps. A follow-up study (Stins et al., 2015) revealed that a forward gait is initiated faster in response to (low-arousing) pleasant compared to unpleasant pictures when participants were instructed to move at image onset; in contrast, the gait was initiated faster in response to unpleasant images when they were to react at image offset. For an explanation, Stins and colleagues proposed that initial processing of unpleasant and threatening items automatically triggers a brief state of immobility ('freezing response') that slows down initiation of gait. After picture processing, however, the initial freezing response ended, and the state of heightened arousal facilitates gait initiation. In sum, studies found that a forward step is more readily initiated on the appearance of pleasant compared to unpleasant stimuli, but temporal dynamics of affective processing is important. Even more important for the present discussion, these studies did not employ the crucial test of disentangling locomotive behavior/gait from the corresponding visual movements towards and away from the objects. Hence, it is still unclear whether the facilitation of gait initiation by affective stimuli was caused by their relation to specific bodily actions (forward/backward steps) or by their relation to a regulation of visuo-spatial distance (approach/retreat motions).

The present research

The present research examined this issue using a virtual reality (VR) setup. Participants wore a VR headset that translated whole-body movements into visual motions in a virtual room (see the example videos in the supplementary material or at OSF). In each trial, a spider or flower appeared in the room and instructions were to move as quickly as possible towards or away from the virtual object with a whole-body movement. Critically, the relationship between the body action and the visual flow produced by that movement was experimentally manipulated: in the *natural optic flow condition*, the forward movement produced a visual approach motion (i.e., a decrease of spatial distance to the target) and the backward movement a visual retreat motion (i.e., an increase of spatial distance to the target). In the *inverted optic flow condition*, this relationship was reversed. Participants experienced both optic flow conditions (in counterbalanced order), and task instructions emphasized the importance of the visual motions. The mapping of stimuli and required visual motion could be either motivationally *congruent* (flower-approach, spider-retreat) or *incongruent* (flower-retreat, spider-approach). Participants completed blocks with both mappings in each optic flow conditions. This setup allowed an orthogonal manipulation of body movements (forward, backward) and visually experienced motions (approach, retreat).

By this dissociation, motivational congruency relations could be defined on the behavioral movement level and on the level of visual approach/retreat motions. According to the *behavior priming hypothesis*, the (appetitive) flower should facilitate the initiation of a forward body movement and the (aversive) spider the initiation of a backward body movement. Statistically, this would be expressed by a two-way interaction between stimulus (flower, spider) and body movement (forward, backward). According to the *distance-regulation priming hypothesis*, this pattern of response facilitation should be observed in the natural optical flow condition; however, it should be reversed, or at least attenuated, in the inverted flow condition. Statistically, this would result in a three-way interaction effect between stimulus, body movement, and visual motion. The larger the reversal (or attenuation) of the response facilitation effect in the inverted flow condition, the smaller should become the statistical two-way interaction effect predicted by the behavior priming hypothesis. By testing the statistical significance of both interaction effects, it can hence be inferred that their magnitudes were different if one effect achieves significance and the other does not. Note, however, that this inference is only valid on the basis of a specific directional hypothesis, because other data patterns could lead to the same statistical outcome. Hence, the direction of the response facilitation effect must be taken into account in addition to the results of the statistical significance tests.

The dependent variables of main interest were the reaction times (i.e., the time between stimulus onset and onset of the body movement) and movement errors (indexing an automatic impulse to move in in a particular direction). Motivational priming should result in faster responses and/or in fewer errors to initiate a movement. The VR movement tracking system also allowed us to analyze movement distance (from the start point to the endpoint in mm) and movement velocity (movement execution time/movement distance). However, these measures were only of secondary interest for the present research hypotheses, because after movement initiation, the body movement was inextricably linked to particular visual changes in the VR environment (e.g., a slower body movement also produced slower motion in the virtual world). Analyses of these performance measures can be assessed in the supplementary information file.

Experiment 1

Participants were seated on a stool and had instructions to approach and retreat from a virtual flower and spider by leaning the upper body forwards or backwards. In the *natural optic flow condition*, the body lean produced a visual motion in the same direction (forward→approach, backwards→retreat); in the *inverted optic flow condition*, this relationship was reversed (forward→retreat, backwards→approach).

Method

Design and sample

The experiment had a 2x2x2 within-design with the factors *Optic flow* (natural, inverted), *Body lean* (forwards, backwards), and *Target* (spider, flower). The order of the optic flow conditions and the order of target-movement (S-R) mappings in each condition were counterbalanced across participants. The study protocol was approved by the local ethics committee (reference no. 2013-14).

In the absence of informed effect size estimates, our smallest effect size of interest was $d = 0.40$ or $\eta^2 = .039$ (for a justification of this choice see Brysbaert, 2019). For Study 1, we collected data from n=43 participants that had sufficient statistical power of .80 for the detection of the hypothesized two-way interaction effects $\eta^2 \geq .026$ and three-way interaction effect $\eta^2 \geq .017$

in a repeated measures ANOVA test (correlation among measures: *r*=.60, nonsphericity correction = 1, calculated with GPower 3.1.9.2). Data from two participants had to be removed due to an excessive frequency of response errors (>25%). Identical exclusion rules were applied to each study (see the supplementary information file).

Apparatus, stimuli, and procedure

Participants wore a VR headset (Oculus Rift DK2) with which they could move around a virtual room that consisted of walls with grid patterns (see the videos in the supplementary material or at OSF). Participants' task was to move as quickly as possible towards or away from a visual object that appeared in the middle of the virtual room. The objects were a flower and a large spider. Both were animated to move slightly in a naturalistic fashion (the flower swayed in the wind, the spider's legs and mandibles twitched). Participants performed body leans as responses. Half of the sample started with the natural optic flow condition, the other half with the inverted flow condition. Two task blocks were performed in each flow condition. For one task block, instructions were to approach the flower and retreat from the spider; for a second task block, instructions were reversed. The order of the task blocks was counterbalanced. After the experiment, participants completed a German version of the Fear of Spiders Questionnaire (Rinck et al., 2002) and questions assessing the difficulty of the task (see the items in the supplement). These questionnaires were included for exploratory reasons.

Task instructions highlighted the importance of the motions towards and away from spiders and flowers in the virtual world. The following task instructions were given for the movement task (translated from German in English language):

For the next task, you should respond as quickly and correctly as possible to a virtual spider and flower that appear in the middle of the room. The trials proceed as follows: at the start of a trial, *an arrow will appear, which will lead you to a centered position. Please adjust your posture until the arrow disappears. After your posture is centered, a spider or flower will appear in the middle of the virtual room, requiring a specific reaction from you:*

- *When you see the spider, approach [retreat from] it as rapidly as possible.*
- *When you see the flower, [approach] retreat from it as rapidly as possible.*

Participants were then asked to repeat the task instruction in own words, and they were corrected if they did not mention the approach/retreat motions in the virtual world.

After having adopted a centered body position at the start of a trial, a spider or flower appeared in the virtual room. Participants were to react as quickly as possible to the target onset with a forward or backward body lean. The body lean was registered when the participant completed the movement and then held position for 1000 ms. Reaction time (RT) was the time interval between stimulus presentation and a forward-backward movement of the headset exceeding 5 cm in forward/backward directions as measured by the Oculus motion tracking system. An error message appeared for 1000 ms when the participant performed an incorrect body lean, did not remain in a final position, or did not respond within 3000 ms. The next trial began 1000 ms after the participant had returned to a straight body position (visually guided by arrows in the virtual world). Each task block consisted of 60 trials (30 spider, 30 flower) that were presented in random order (total: 2×2×60=240 trials).

Results

Data preparation and supplementary analyses are reported in the supplement. Table S1 in the supplement also reports descriptive data as a function of the conditions. Error proportions were log-transformed before analyses; however, descriptives indicate untransformed values for ease of interpretation.

Reaction times were subjected to a 2×2×2×2×4 mixed ANOVA with the within-factors *Target* (flower, spider), *Body lean* (forward, backward), and *Optic flow* (natural, inverted), and counterbalanced *Order of the optic flow conditions* (natural first, inverted first) and *Order of S-R mappings* in each optic flow condition (4 levels) as group factors. The two-way interaction between *Target* and *Body lean* was significant, $F(1, 33) = 9.63$, $p = .004$, $\eta_p^2 = .226$; importantly, this interaction effect was not qualified by *Optic flow,* $F(1, 33) = 0.90$, $p = .351$, $\eta_p^2 = .026$. As shown in Figure 1, forward leans in response to flowers ($M = 1020$ ms, $SE = 25$) and backward leans in response to spiders ($M = 1017$ ms, $SE = 22$) were facilitated relative to the reversed mappings (flower: $M = 1096$ ms, $SE = 23$, spider: $M = 990$ ms, $SE = 25$). Follow-up comparisons showed that the *Target×Body lean* interaction was significant in the natural optic flow condition, $F(1, 33) = 9.94$, $p = .003$, $\eta_p^2 = .231$, but not in the inverted optic flow condition, $F(1, 33) = 2.12$, $p = .155$, $\eta_p^2 = .060$. In the omnibus ANOVA, the main effect of *Target* (faster reactions to spiders), $F(1,33) = 86.74$, $p < .001$, $\eta_p^2 = .724$; the main effect of *Body lean* (faster forward leans), $F(1, 33) = 45.81$, $p < .001$, $\eta_p^2 = .581$; and the *Target×Body lean×Order of S-R mappings* were also significant, $F(3, 33) = 4.07$, $p = .014$, $\eta_p^2 = .270$.

In a corresponding ANOVA of the (log-transformed) proportions of movement errors, no effect reached significance, including the *Target×Body lean* interaction effect, $F(1, 33) = 1.90$, $p = .177$, $\eta_p^2 = .054$, and the *Target×Body lean×Optic flow* interaction effect, $F(1, 33) = 0.20$, $p = .658$, $\eta_p^2 = .006$.

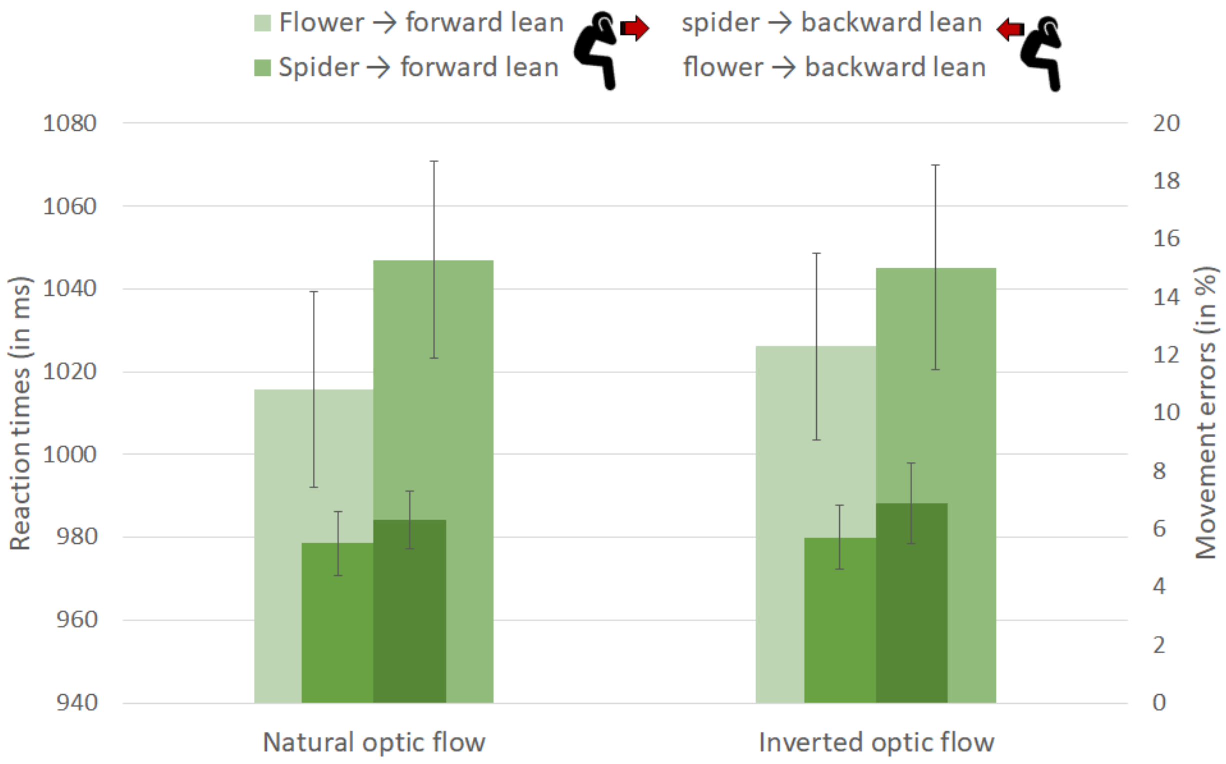

Figure 1. Reaction times (large bars) and error rates (small bars) of body leans as a function of target and optic flow conditions in Experiment 1. Error bars show the standard error of the means.

Discussion

In Study 1, a forward lean was initiated faster in response to a flower, and a backward lean faster in response to a spider, than vice versa. This pattern of facilitation supports the behavior priming hypothesis, which predicted a grounding of approach/avoidance motivations in forward/backward actions of the body. The *Target×Body lean* interaction effect was however only significant in the natural optic flow condition, and not in the inverted optic flow condition. Thus, it remains unclear whether a sensorimotor grounding in whole-body movements can override motivations to regulate the distance to appetitive/aversive stimuli. For a stronger test, we therefore repeated the experiment with instructions of whole-body forward/backward steps that are most characteristic of pedal locomotive behavior in humans.

Experiment 2

Study 2 was identical to Study 1 with the major change that participants performed whole-body forward/backward steps in response to the virtual objects. Based on the hypothesis of a strong sensorimotor grounding in pedal locomotion, we expected that flowers facilitate forward steps and spiders backward stepping in both optic flow conditions.

Method

Design, stimuli, and procedures were identical with Study 1, with the difference that participants performed body steps. We also made minor tweaks to the grid walls to improve the corridor illusion. Movement initiation was registered when the headset was moved more than 14 cm in the forward or backward direction as tracked by the Oculus VR system.

Study 1 yielded a large behavior priming effect ($\eta_p^2 = .226$); for Study 2, we collected data from $n = 30$ (17 female) that provided sufficient statistical power of .80 for the detection of hypothesized two-way interaction $\eta^2 \geq .037$ and three-way interaction effects $\eta^2 \geq .024$ in a repeated measures ANOVA (correlation among measures: r=.60, nonsphericity correction = 1, calculated with GPower 3.1.9.2). Data from five participants had to be removed due to the preset criterion of an excessive high number of movement errors (>25%).

Results

Data preparation, outlier removal procedures, and supplementary analyses are reported in the supplement. Table S2 in the supplement also contains the mean RTs and error rates in each condition.

In the 2×2×2×2×4 ANOVA of the RTs, the *Target*×*Body step* interaction was significant, $F(1, 17) = 10.16$, $p = .005$, $\eta_p^2 = .374$; the *Target*×*Body step*×*Optic flow* interaction was not significant, $F(1, 17) = 0.19$, $p = .665$, $\eta_p^2 = .011$. As shown in Figure 2, a forward step in response to flowers (M = 1214 ms, SE = 30) and a backward step in response to spiders (M = 1238 ms, SE = 34) were initiated faster than vice versa (flower: M = 1327 ms, SE = 24, spider: M = 1197 ms, SE = 24). Planned tests confirmed significant *Target*×*Body step* interaction effects in the natural optic flow, $F(1, 17) = 5.77$, $p = .028$, $\eta_p^2 = .253$, and in the inverted optic flow conditions, $F(1, 17) = 4.99$, $p = .039$, $\eta_p^2 = .227$. In the omnibus ANOVA, the main effect of *Body step* (faster forward step), $F(1, 17) = 14.94$, $p < .001$, $\eta_p^2 = .468$, and the main effect of *Target* (faster reactions to spiders) , $F(1, 17) = 21.76$, $p < .001$, $\eta_p^2 = .561$, were also significant. The main effect of *Optic flow* (faster reactions with natural optic flow) did not reach significance, $F(1, 17) = 4.37$, $p = .052$, $\eta_p^2 = .205$.

In the ANOVA of the (log-transformed) error rates, the *Target*×*Body step*, $F(1, 17) = 0.35$, $p = .854$, $\eta_p^2 = .002$, and the *Target*×*Body step*×*Optic flow* effects, $F(1, 17) = 0.89$, $p = .360$, $\eta_p^2 = .049$, were not significant.

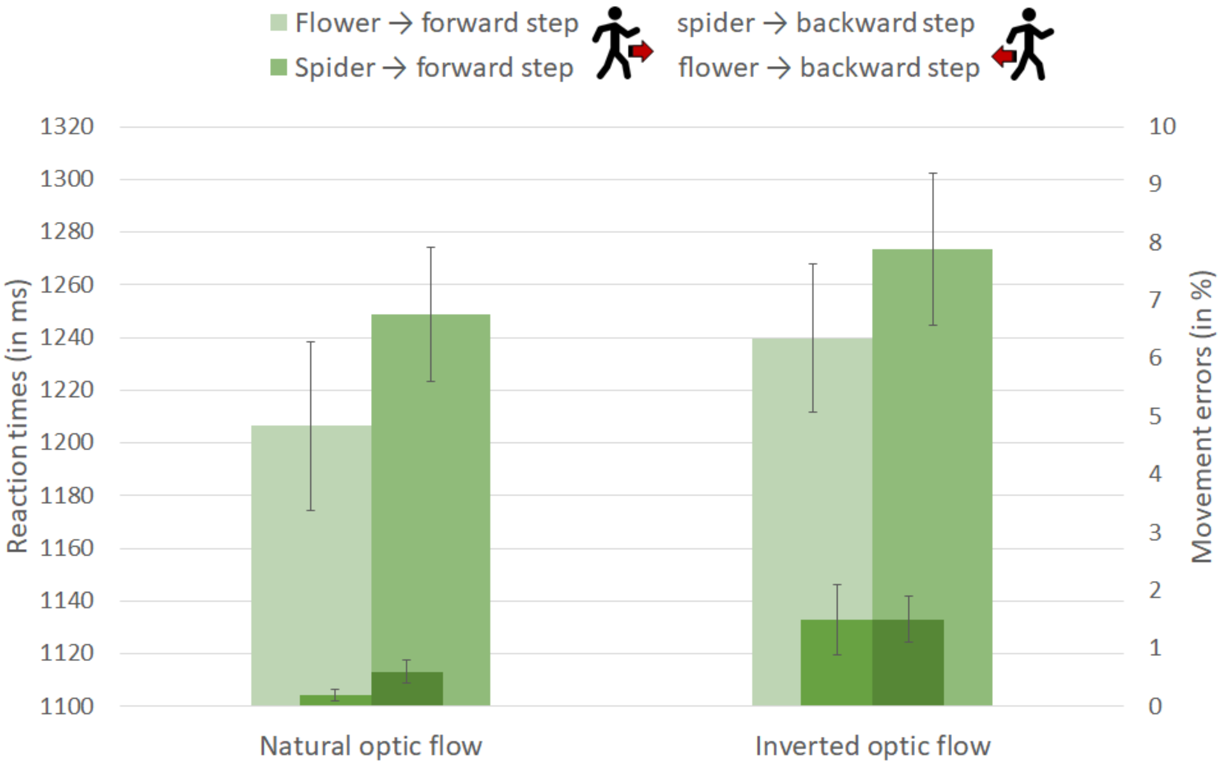

Figure 2. Reaction times (large bars) and error rates (small bars) of body steps as a function of target and optic flow conditions in Experiment 2. Error bars show the standard error of the means.

Discussion

Experiment 2 reproduced the results of our first study, again supporting the behavior priming hypothesis. In this experiment, initiation of whole-body movement was facilitated even when the forward step was linked to a motion away from the (appetitive) flower and the backward step to a motion towards the (aversive) spider in the virtual world. Together, these results suggest that approach/avoidance motivations are closely linked to forward/backward body movements, producing a propensity for action that requires time to overcome.

Experiment 3

Although task goals were explicitly instructed in terms of the visual motion in the virtual world, it is possible that participants ignored these visual motions during action selection in order to simplify the task rules for themselves. For example, they could have simplified the task rule: "When I see a spider, I should approach it with a backward step" to the rule: "When I see a spider, I should perform a backward step." This internal task recoding could have directed participants' attention away from the production of specific motions in the virtual world (e.g., approach of a spider), highlighting instead the production of a specific body step (e.g., stepping backwards), which would explain why (whole) body movements were more influential than visual motions in this set of studies. Note that this account implies a flexible weighting of visual and motor features of the task that tailor perception and action to the situation at hand (Memelink & Hommel, 2013). For a test of this weighting-mechanism, we therefore implemented a task procedure in Experiment 3 that enforced attention to the production of visual approach/retreat motions in the virtual world. Specifically, participants were asked to perform body steps to the words APPROACH and AVOID in a randomly intermixed subset of trials. For correct performance in these trials, the forward/backward step must be translated into a corresponding visual motion in the virtual word, which implies, that the visual motion is actively intended in these trials. Based on previous studies using similar task procedures (Eder & Rothermund, 2008; Theeuwes et al., 2015), we expected that the intention is also maintained during trials with spiders and flowers as targets, promoting a motivational congruency with the intended visual motion (van Dantzig et al., 2008). Accordingly, a Target×Body step×Optic flow interaction effect was hypothesized for this experiment. Alternatively, it is possible that whole-body movements are rigidly linked to appetitive/aversive motivations due to a biological hardwiring and/or countless repetitions over lifetime (Konorski, 1967). In this case, task-induced intentions to produce visual motions in the virtual world should have no effect on the initiation of the body steps, reproducing the result of our previous experiments.

Method

Design, stimuli, and procedure were identical with Study 2, with the difference that participants additionally responded to the words APPROACH and AVOID in a subset of trials. The word was displayed as 3D text at the same place as the flower/spider. Participants were instructed to approach the word APPROACH and to retreat from the word AVOID as quickly as possible. Each optic flow condition started with a training block in which participants practiced movements to the words (10 APPROACH, 10 AVOIDANCE) in random order. Analogous trials were randomly intermixed in the subsequent task blocks (10 APPROACH, 10 AVOIDANCE, 30 flower, 30 spider). Study 2 produced a very large behavior priming effect (η_p^2 = .374); for Study 3, we collected data from *n*=32 (22 female) that provided sufficient statistical power of .80 for the detection of hypothesized two-way interaction $\eta^2 \geq .037$ and three-way interaction effects $\eta^2 \geq .034$ in a repeated measures ANOVA (correlation among measures: *r*=.60, nonsphericity correction = 1, calculated with GPower 3.1.9.2). No participant had to be excluded based on our error outlier criterion (≥ 25%).

Results

Data preparation, outlier removal procedures, mean data (Table S7), and detailed statistical results are reported in the supplement.

Analyses of the performance in the experimental trials with spiders/flowers as target stimuli are shown in Figure 3. In the 2×2×2×2×4 ANOVA of the RTs, the interaction between *Target* and *Body step*, *F*(1, 24) = 0.93, *p* = .346, η_p^2= .037; and the *Target*×*Body step*×*Optic flow* interaction effect, *F*(1, 24) = 1.35, p = .256, η_p^2= .053, were not significant. The main effects of *Body step* (faster forward step), *F*(1, 24) = 39.48, $p < .001$, η_p^2= .622; *Target* (faster reaction to spiders), *F*(1, 24) = 25.82, $p < .001$, η_p^2= .518; and *Optic flow* (faster reaction with natural optic flow), *F*(1, 24) = 17.35, $p < .001$, η_p^2= .420, were however significant.

In the ANOVA of (log-transformed) movement errors, the *Target*×*Body step* interaction effect was not significant, *F*(1, 24) = 0.30, p = .592, η_p^2= .012; the three-way interaction effect with counterbalanced order of optic flow conditions reached significance, *F*(1, 24) = 5.79, p = .024, η_p^2= .194. Backward stepping in reaction to spiders and forward stepping in response to flowers were more accurate than vice versa when the task started with the inverted optic flow condition. Most important, the *Target*×*Body step*×*Optic flow* interaction effect was significant, *F*(1, 24) = 10.35, p = .004, η_p^2= .301. In the inverted flow condition, backward stepping (*M* = 2.8%, *SE* = 0.9) was more difficult than forward stepping (*M* = 1.3%, *SE* = 0.6) in response to spiders, whereas forward stepping (*M* = 3.0%, *SE* = 0.9) was more difficult than backward stepping (*M* = 1.4%, *SE* = 0.4) in response to flowers, *F*(1, 24) = 8.66, p = .007, η_p^2= .265. In the natural optic flow condition, this pattern of response facilitation was non-significantly reversed, *F*(1, 24) = 3.15, p = .089, η_p^2= .116 (see Fig. 3).

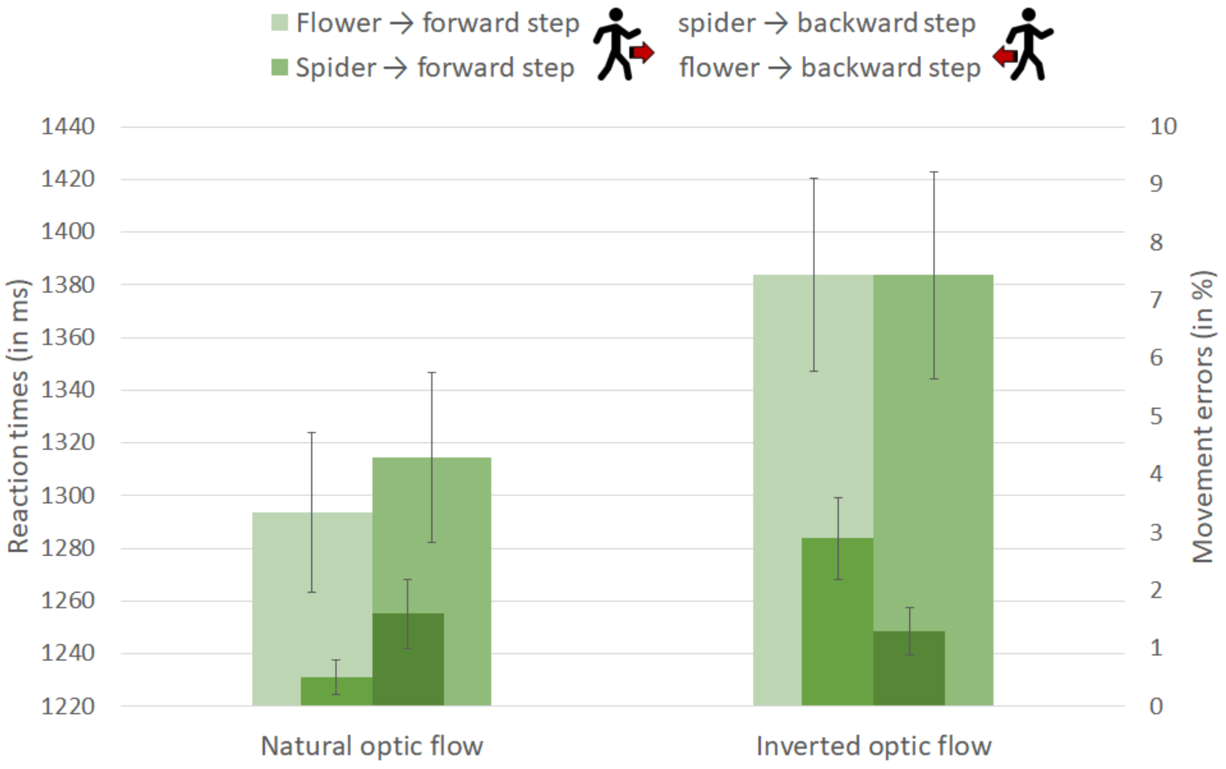

Figure 3. Reaction times (large bars) and error rates (small bars) for body steps in Study 3 as a function of target and optic flow conditions. Error bars show the standard error of the mean.

Analyses of response accuracy (error rates) in the intermixed training trials with words as target stimuli showed that it was easier for participants to perform a forward step in response to the word APPROACH and a backward step in response to the word AVOIDANCE (*M* = 2.4%, *SD* = 3.1) than vice versa in the inverted condition (*M* = 5.9%, *SD* = 6.1), *t*(31) = 2.97, *p* = .006, d_z = 0.52. This difference confirms that participants had difficulties to perform an approach motion with a backward step and an avoidance motion with a forward step even after substantial action training.

Discussion

The results support the distance-regulation priming hypothesis over the behavior priming hypothesis. In the RT measure, neither hypothesis was supported. It is remarkable, however, that the intermixing of a few trials that directed participants' attention to the visual action effect was enough to reduce the large behavioral priming effect (η_p^2=.374) obtained in Study 2 to a (non-significant) effect of negligible magnitude (η_p^2=.037). In contrast, the error data clearly supported the distance regulation hypothesis. We can only speculate about the reasons why the interaction effect only showed up in the error measure. Response latencies were generally slower, and error rates higher, in comparison to Study 2, which suggest that the randomly intermixed practice trials increased the difficulty of the task. It is also known that priming effects become concentrated on one measure when lower speed is traded for a gain in accuracy, and vice versa (Draine & Greenwald, 1998). In short, predictions are not always clear what performance measure will be most affected in a priming task, which was the reason why both performance measures were analyzed in the first place.

Experiment 4

The present results suggest that appetitive/aversive motivations have a stronger sensorimotor grounding in whole-body movements than manual actions because the latter can be more variably linked to approach/avoidance motions. For a test of this explanation, we conducted an experiment that was identical to Study 2 except that the motion in the virtual world was controlled with thumbstick movements on a gamepad. Based on the hypothesis that approach/avoidance-related manual actions are less affected by preexisting sensorimotor associations, we hypothesized that behavioral performance is primarily controlled by the intended motion in the virtual world, resulting in a statistical *Target×Thumbstick movement×Optic flow* interaction effect.

Method

Design, stimuli, and procedures were identical with Study 2, with the difference that participants performed thumbstick movements with an Xbox gamepad controller connected to the PC. Movement initiation was registered when the thumbstick left the center position of the gamepad.

For this experiment, we collected data from N = 50 (35 female), as the magnitude of priming effects obtained with manual actions could be smaller. The pre-registered sample size had sufficient power of .80 to detect hypothesized two-way interaction effects with $\eta^2 \geq .022$ and three-way interaction effects with $\eta^2 \geq .012$ in a repeated measures ANOVA (correlation among measures: r=.60, nonsphericity correction = 1, calculated with GPower 3.1.9.2). One data set was removed due to an excessive high number of errors (>25%); an additional data set was lost due to a technical error during the experiment. Hypotheses and study plan were pre-registered at OSF.

Results

Data preparation, outlier removal procedures, and mean data (Table S4) are reported in the supplement.

In the ANOVA of the RTs, the interaction between *Target* and *Thumbstick movement* was not significant, $F(1, 40) = 0.52, p = .474, \eta_p^2 = .013$. The *Target×Thumbstick movement×Optic flow* effect was also not significant, $F(1, 40) = 4.07, p = .050, \eta_p^2 = .092$. Planned comparisons showed a significant *Target×Thumbstick movement* interaction effect in the natural optic flow condition, $F(1, 40) = 4.17, p = .048, \eta_p^2 = .094$, indicating faster initiation of a backward motion (thumbstick pull; M = 501 ms, SE = 11) than a forward motion (thumbstick push; M = 531 ms, SE = 13) in response to spiders, and no difference in responses to flowers (forward: $M = 534$ ms, $SE = 10$; backward: $M = 529$ ms, $SE = 11$). This pattern was non-significantly reversed in the inverted optic flow condition, $F(1, 40) = 0.84$, $p = .365$, $\eta_p^2 = .021$ (see Fig. 4). In the omnibus ANOVA, the main effects of *Thumbstick movement* (faster pull), $F(1, 40) = 25.87$, $p < .001$, $\eta_p^2 = .393$; *Target* (faster reactions to spiders), $F(1, 40) = 19.43$, $p < .001$, $\eta_p^2 = .327$; and *Optic flow* (faster reactions with natural optic flow), $F(1, 40) = 13.28$, $p = .001$, $\eta_p^2 = .249$, were also significant.

In the ANOVA of the (log-transformed) error rates, the *Target*×*Thumbstick movement* interaction effect was not significant, $F(1, 40) = 1.14$, $p = .292$, $\eta_p^2 = .028$; however, the *Target*×*Thumbstick movement*×*Optic flow* effect was, $F(1, 40) = 6.16$, $p = .017$, $\eta_p^2 = .133$. As shown in Figure 4, participants made less errors in the natural flow condition when they approached the flower with a thumbstick push ($M = 5.3\%$, $SE = 1.0$) and retreated from the spider with a thumbstick pull ($M = 3.5\%$, $SE = 0.9$) than vice versa (flower-pull: $M = 5.2\%$, $SE = 0.9$; spider-push: $M = 5.3\%$, $SE = 1.3$). This effect was however not significant, $F(1, 40) = 2.53$, $p = .120$, $\eta_p^2 = .059$; in contrast, the pattern of response facilitation was significantly reversed by the inverted optic flow in which pulling the thumbstick backwards effected approach (spider: $M = 5.3\%$, $SE = 0.9$; flower: $M = 4.7\%$, $SE = 0.8$) and forward pushing effected retreat (spider: $M = 4.7\%$, $SE = 0.7$; flower: $M = 7.4\%$, $SE = 0.8$) and, $F(1, 40) = 5.16$, $p = .029$, $\eta_p^2 = .114$. In the omnibus ANOVA, the main effect of *Target* (fewer erroneous reactions to spiders) was also significant, $F(1, 40) = 7.48$, $p = .009$, $\eta_p^2 = .158$.

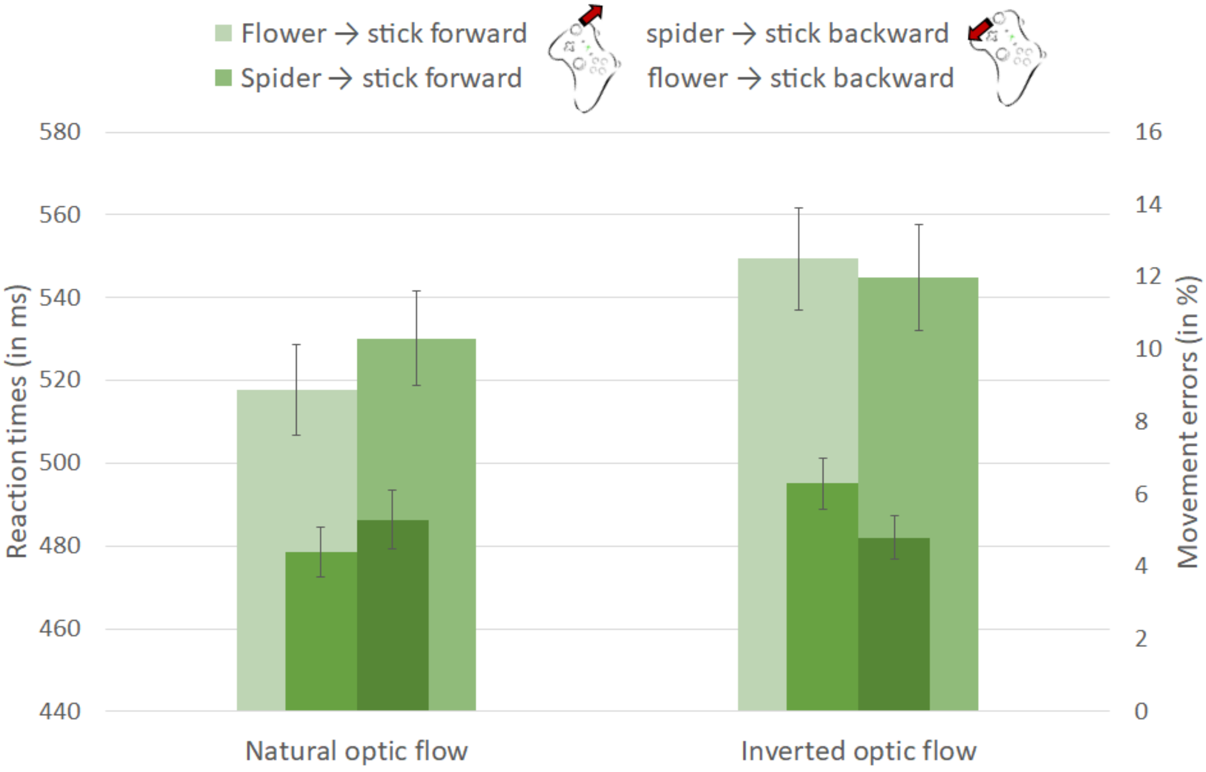

Figure 4. Reaction times (large bars) and error rates (small bars) of thumbstick movements as a function of target and optic flow conditions in Experiment 4. Error bars show the standard error of the means.

Discussion

Results supported the hypothesis that the movement of the hand is influenced more strongly by the anticipated approach/avoidance motions in the virtual world than by the direction of hand movement. While the pattern of behavior facilitation was not significant in the RT measure according to the conventional statistical significance criterion ($p < .05$), a significant priming effect was observed in the error measure. In comparison to the results of Study 2, it thus seems that forward/backward movements of the hand could be mapped more easily onto approach/avoidance motions than corresponding whole-body movements. This conclusion is also in line with previous studies that observed no effect of arm flexion/extension on motivational action tendencies (for a meta-analysis see Laham et al., 2015).

General Discussion

Four experiments (*N*=155) investigated a sensorimotor grounding of approach-avoidance motivations in whole-body locomotive behavior. Using a VR setup, participants were faster to initiate a forward movement of the body in response to a flower and a backward movement in response to a spider than vice versa. This pattern of action facilitation was observed with forward/backward leans of the upper body in Study 1, and with forward/backward stepping in Study 2, even when a forward step produced a motion away from the spider and a backward step in a motion towards the flower in the virtual world. These results are in line with the hypothesis that approach motivation is grounded in forward locomotion, and retreat in backward locomotion, presumably due to countless sensory-motor interactions of this type with the world over a lifetime of experiences. A sensorimotor grounding can also explain why people often react inappropriately in situations in which they must not retreat from the source of threat (e.g., in interactions with aggressive dogs).

Study 3 additionally showed that the prioritized link to locomotive reaction is not fixed but, rather, affected by attention and training. Specifically, participants in the inverted optic flow condition made fewer errors to retreat from a spider with a forward step and to approach the flower with a backward step (than vice versa) following explicit training to approach the target with a backward step and to retreat from it with a forward step. It is plausible that the intermixed training trials directed participants' attention to the visual (approach/retreat) motion in the virtual world, which increased the saliency of these visual action effects for action control (Memelink & Hommel, 2013). The behavior training in Study 3 hence promoted action guidance by visual action effects in the virtual world, while plain instruction of such guidance in Study 2, in the absence of a behavioral training, was not sufficient. This also fits with other studies that found instruction effects on automatic response activations only after active preparation for the task (Meiran et al., 2017; see also Theeuwes et al., 2015).

Visual distance-regulations in the virtual world also influenced motivational action tendencies in Study 4 in which these motions were controlled manually with movements of a thumbstick, while the forward/backward direction of the hand movement had no effect. This result was expected based on previous studies that found no evidence for a strong embodiment of approach- and avoidance-related actions performed with the arm (e.g., Markman & Brendl, 2005) and fingers (e.g., Wickens, 1938). Overall, the results hence confirm that manual behaviors can be flexibly used, whereas locomotion is more rigidly linked to motivational states.

The important implication is that the body, and how the body was used in previous interactions, plays a crucial role for the instigation of approach/avoidance tendencies. While others before us have highlighted the embodiment of approach/avoidance states (e.g., Harmon-Jones, Price, & Harmon-Jones, 2014), conclusive evidence for a grounding in whole-body movement was missing, due to the fact that locomotive behavior is typically confounded with particular visual changes. In fact, Rougier and colleagues (2018) showed that visual cues of whole-body locomotion can trigger approach-avoidance tendencies even if the participant was stationary. Our VR setup was an effective tool to disentangle these factors, showing that whole-body locomotion can dominate over visual approach/avoidance cues if both are in conflict.

The present evidence for a sensorimotor grounding in locomotive behavior has implications for theories and measurement procedures. Concerning measurement procedures, the present findings advise caution in the use of highly symbolic tasks that make exclusive use of manual actions (e.g., keypresses). While these laboratory tasks often produced strong and reliable effects (Krieglmeyer & Deutsch, 2010), they might underestimate the role of body-based processes that motivate behavior outside of the laboratory task. For example, walking to a cocktail bar requires different body-based simulations than drinking the cocktail, which must be considered in the analysis of both types of (approach) behaviors. Instead of using a one-size-fits-all measurement approach, researchers should therefore analyze carefully whether the behavior performed in the laboratory task will correspond with the behavior of interest. A VR setup could be a promising tool for a methodological advancement in this direction.

In respect to theory, explanations of approach-avoidance motivation must integrate body-related factors for a complete account. A straightforward account could be that the human animal, similar to Hershberger's chicken, has a biological disposition for a forward locomotion in appetitive contexts and for a backward locomotion in aversive situations. According to this account, locomotion would be an embodied reaction to appetitive/aversive stimulations—analogous to the concept "unconditional/conditioned reflex" promulgated by early behaviorists (e.g., Konorski, 1967) and still upheld in modern theorizing about motivational "stimuli" (or appraisals thereof) that trigger automatic reactions (e.g., Krieglmeyer et al., 2013; Lang, 1995). While the parsimony of this account is captivating, its anti-cognitivistic attitude makes it difficult to understand how factors such as task instructions and attention can change these supposedly hardwired action tendencies, as observed in Study 3. Furthermore, in the absence of a detailed mechanistic model, no new hypotheses could be derived that would render this account falsifiable.

Another account, dating back to the early work of Kurt Lewin (1935) and formally described by cybernetic control theory (Carver & Scheier, 1998), views approach behavior grounded in the function of decreasing the distance between the target and the self, and avoidance in increasing that distance. The distance to the target, and the behavioral means of distance regulation, are cognitively simulated (Barsalou, 2002; Jeannerod, 2001), grounding approach/avoidance in sensorimotor simulations of distance changes (Neumann & Strack, 2000). If previous sensorimotor interactions are integrated into simulations of locomotive behavior, as demonstrated in studies on motor imagery (e.g., Kunz, Creem-Regehr, & Thompson, 2009), the account can explain why the simulation of a forward movement that resulted in a movement away from the spider consumed more time than the corresponding simulation of a backward movement. Wayne Hershberger (1986) adapted cybernetic theory to explain the learning difficulties of his 4-day old chickens to approach the food cup by running away from it. A cognitively enriched version of this account could also explain the present data with humans.

A perceptual control theory of embodied motivated action

More specifically, we suggest that locomotion, like any other goal-directed activity, is guided by multisensory perceptual representations of the environment, including bodily signals. In fact, investigations of walking in humans, cats and insects, of flight in insects and of swimming in fish have demonstrated that the timing and magnitude of the locomotor activity is strongly influenced by reafferent sensory signals from receptors that become phasically activated during locomotion (for reviews see Pearson et al., 2006; and Rossignol et al., 2006). The feedback originates from muscles and skin afferents as well as from special senses (vision, audition, vestibular) and it adapts the locomotor pattern dynamically to the requirements of the environment. In terms of cybernetic control theory, the perception-action loop is closed: the locomotor activity changes the surrounding environment, including bodily reafference, and the perception of the new situation prompts readjustments of the locomotor activity. Locomotion will stop when the perceived situation matches the wanted situation that was set as a reference signal (or “goal”) for the activity. In the case of an approach-motivated locomotion, the reference which should be a position in reach to a wanted target, and in the case of an avoidance motivation, a position out of reach, representing safety. In the present studies, these wanted end-positions were set externally via task instructions, but motivational processes can also set them internally (Carver & Scheier, 1998).

As shown in Figure 5, cybernetic action control consequently requires cognitive systems that process afferent sensory signals from the surrounding (input function), compare these signals with the wanted end-states (comparison function), and modify behavior to reduce these discrepancies (output function). This means sensory signals ($s_1..s_n$) must be somehow translated into motor command signals ($m_1..m_n$) that adapt the perceived situation to the current needs (the reference signal). An elegant solution to this "translation problem" was suggested by the Theory of Event Coding (TEC), which claims that action and perception have a commensurable representational format (Hommel et al., 2001). If action control is based on a cognitive representation of a wanted situation or event, reafferent perceptual signals from the current situation can be directly compared with the percept of the anticipated situation that serves as a reference signal for the action. According to this account, the purpose of behavior is to produce a wanted perception, or as Powers (1973) succinctly phrased it: behavior IS the control of perception.

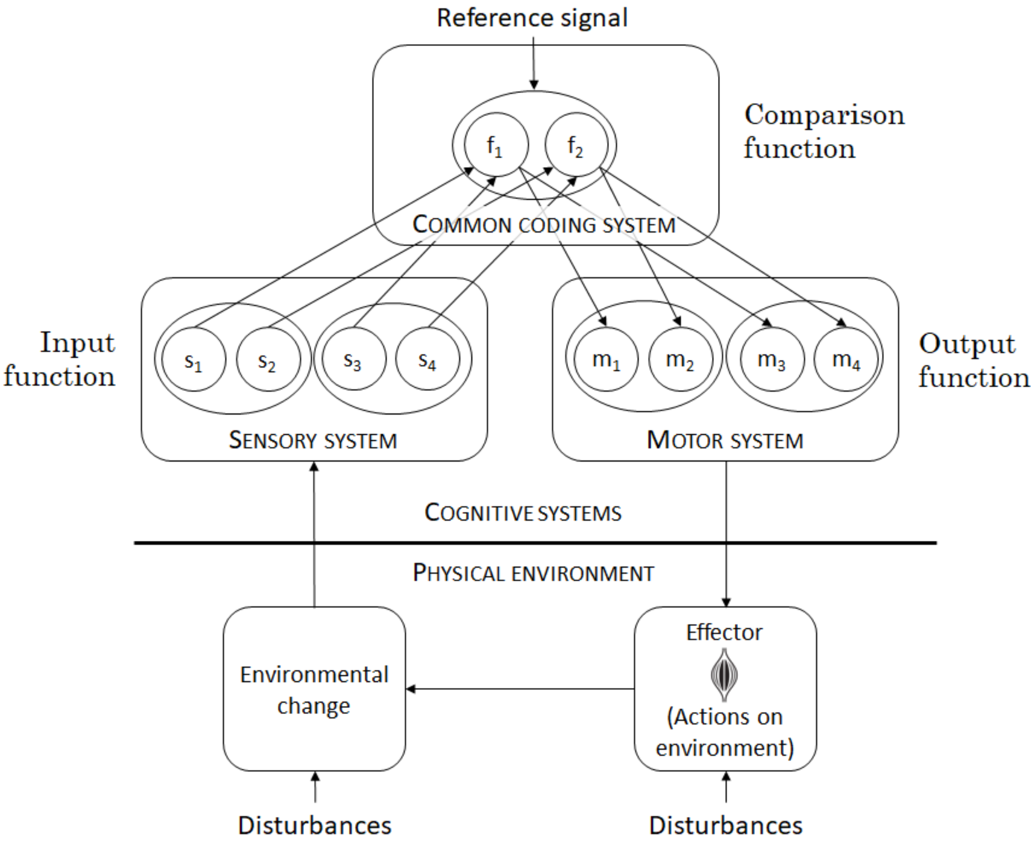

Figure 5. Perceptual control theory of motivated action (adapted from Hommel et al., 2001, and Powers, 1973). $S_1..S_n$ = sensory codes, $M_1..M_n$ = motor codes, $F_1..F_n$ = feature codes

Motivation affects action selection because comparisons of perceived and to-be-produced situations are not made holistically but on feature dimensions (or codes) that are most important to us (Memelink & Hommel, 2013). For example, spatial distance information will be important when seeking shelter from a dangerous animal, but it is likely much less important if one hastily attempts to rescue one's financial deposits during a great stock market crash. Feature dimensions refer to perceptual primitives (color, shape, intensity, etc.) and can include complex perceptual categories (e.g., the perception of a person's ethnicity) that are grounded in these perceptual primitives (Barsalou, 1999; Schyns et al., 1998). Motivational weightings of need-relevant feature dimensions, and memories from previous action episodes (Logan, 1988), can help to narrow down the potentially infinite set of behavioral possibilities to a specific action that has a capacity to produce the wanted perceptual event in this situation.

According to this analysis, perceptual goals can hence also refer to selected proprioceptive signals produced by one's own body movements. For the whole-body movements in the present studies, such proprioceptive signals could have been provided by vestibular senses, perceived contractions of joints and muscles, and the proprioception of foot contact with the ground. This cluster of proprioception could be differentiated from signals from other senses, such as the visual perception of the (virtual) world. Assuming flexibility in the weighting of sensory signals (for evidence see e.g., Thébault et al., 2020), proprioception of the whole-body movement (f1) could have been weighted stronger than visual perceptions (f2) in Study 1 and Study 2, because this weighting reduced the complexity of the task (for a justification of this assumption see our introduction to Study 3). Consequently, discrepancies to f1 were monitored more closely than discrepancies to f2 in this set of studies, minimizing the influence of visual action effects. In Experiment 3, by contrast, the intermixed training trials enforced attention to the visual action effects, presumably increasing the weights of f2 relative to f1. It is also plausible that proprioceptive signals from movements of a thumbstick were markedly reduced compared to those of whole-body movements, reducing the weights of f1 relative to f2. As a result, visual action effects had a larger influence on action control in this set of two studies.

Flexible weightings of perceptions across and within modalities can thus explain why whole-body movements were more influential in a subset of our studies but not in the other. However, it does not explain why flowers and spiders facilitated forward and backward motions of the body or in vision. A reasonable assumption, outlined in more detail by Cziko (1997), could be that perceptual control systems that were useful for the human species to the securement of nourishment and mating, or for protection against threats and dangers, have evolved through a Darwinian natural selection process. Many students of animal behavior argued that complex, so-called "instinctive" behaviors must have an evolutionary basis, because all the individuals of the species are somehow able to perform them without first experiencing the behaviors performed by others or being in any way instructed (Lorenz, 1981). For example, a mother rat will build a nest and groom her young even if she was raised in total isolation from other female rats (Rosenblatt, 1969). It is hence possible that appetitive/aversive control systems have analogously evolved in the human species that serve a purpose to establish contact with wanted objects such as food or mates, and to avoid contact with threatening object such as toxins or predators. Note that according to this account, control systems only could be inherited, while the subserving behavior is not. Or as William Powers (cited in Cziko, 1997, p. 115) phrased it: "There's no way to inherit behavioral outputs, because the outputs must remain adjustable to current circumstances, which never repeat exactly. All that can be inherited are control systems, and at the highest existing level perhaps some reference signals."

Complementary to a behavior organization by biological design is ontogenetic learning through direct or vicarious experience. Given the human body plan with its orientation of limbs, perceptual organs, and the musculoskeletal system to movements in the anterior direction, it is very likely that adults have experienced countless episodes during their lifetime in which they approached desired objects with a forward motion and avoided undesired ones by moving backwards or at least by withholding a forward movement. These episodes should have left memory traces in the cognitive systems by strengthening those perceptual control systems that served the purpose of approach and avoidance best in the individual's history. One way how this strengthening could operate is by forming memories of the output function: relations between specific movement patterns (or more precisely: motor codes thereof) and their perceptual effects on the environment (see the right side in Fig 5). If these action-perception links are bi-directional, as suggested by the closed loop in our model, memories of perceptual effects can be used in search for actions that are appropriate to produce a wanted perceptual effect. In support of this assumption, numerous studies showed that the cognitive activation of a perceptual action effect, either endogenously by thinking or exogenously by perceptual registration, automatically primes the associated movement pattern (for reviews of this 'ideo-motor hypothesis' see Hommel et al., 2001; Nattkemper et al., 2010; Shin et al., 2010). Studies also showed that action-effect learning is enhanced for sensory effects that were reliably produced (Elsner & Hommel, 2004) and rewarding for the individual (Eder et al., 2019).

If the purpose of a control system is to establish contact with wanted targets, and if movements in a forward direction were serving better this purpose, then stronger links should be formed between wanted targets and forward movements compared to backward movements. If different effectors are used for the control of approach (e.g., walking to a good friend and greeting him with a handshake), then directional codes specifying a forward direction should become abstracted from the use of particular effectors, and feature codes specifying a forward direction should have more weight in the search for action compared to other directional codes. Conversely, if the purpose of the control system was to prevent contact with a threatening object, and backward motions served this purpose better, then feature codes specifying a backward direction should be weighted more. Note that directional codes (e.g., forward-backward, left-right, etc.) alone cannot specify the appropriate action, because this requires additional specification of perceptual effects related to the effector (e.g., hand for a greeting handshake), side of limb (e.g., use of the right hand), amplitude and force, etc. By assembling a set of specifications in the common coding area, the anticipation of a wanted perceptual action effect should be sufficiently precise to narrow down a set of potential candidate movements to a single action, which is then executed by the motor system. In many situations, parametrization of the necessary action via specification of wanted perceptual effects should be easy and could be done very rapidly, as it is typically observed with locomotion from one place to another. Furthermore, action plans from previous episodes, once formed in the common coding area, could be reused for future use in similar situations (see e.g., Giesen & Rothermund, 2016). These mental short-cuts would allow for rapid initiation of movements, as it is typical for highly motivated or skilled behavior, whilst preserving a degree of cognitive flexibility that is necessary for behavioral adaptations to the situation at hand.

To sum this account up, control of approach-avoidance behavior is grounded in cognitive anticipations of wanted perceptual action effects that specify necessary movements to produce these wanted effects. That means, the purpose of behavior is to create a specific perceptual state (Powers, 1973), which could be: making contact with a wanted object in the case approach, and abandoning, or preventing contact with unwanted objects in the case of avoidance. Perceptual control systems dedicated to approach and avoidance likely evolved through a Darwinian natural selection process, and are hence hypothesized to be universal to the members of our species (Cziko, 1997). Their operation is however modified by cognitive processes, such as feature weighting, that tailor perception and action to individual needs and affordances of the current situation (Hommel et al., 2001). Conceptualized in this way, perceptual control systems of approach/avoidance hence correspond with the historical idea of aversive/appetitive motivation systems that (neo)behaviorists invented for an account of motivated behavior (Konorski, 1967); in contrast to these accounts, however, the perceptual control theory emphasizes the circularity of the perception-action loop, according to which action causes perception and vice versa.

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Author contributions

AE developed the study concept. All authors contributed to the study design. AS programmed the experiment. Testing and data collection were performed by research assistants supervised by AK. AE and AK performed the data analyses. AE drafted the manuscript and the co-authors provided critical revisions. All authors approved the final version of the manuscript for submission.

Supplemental Material

Data analysis and outlier identification procedures

Data sets with an excessive high number of response errors (>25%) were removed from analyses. The first 9 trials in each task block were removed as practice trials. Following the recommendation of Tukey (1977), RTs that were 1.5 interquartiles above the third quartile or below the first quartile of the participant's RT distribution in each optic flow condition were removed before RT analyses. This criterion removed M = 7.5% latencies from Study 1, 5.1% from Study 2, 8.8% from Study 3, and 4.9% from Study 4. We analyzed RTs from correct responses and (log-transformed) error proportions (reported in the main paper); movement distance (from start point to end point in mm); and movement velocity (movement distance/movement execution time in ms). Dependent variables were analyzed using a mixed 2×2×2×2×4 analysis of variance (ANOVA) with the within-factors *Optic flow* (natural, inverted), *Body movement* (forwards, backwards), and *Target* (spider, flower), and the group factors *Order of the optic flow conditions* (natural first, inverted first) and *Order of target-movement (S-R) mappings in the optic flow condition* (4 levels).

Study 1

Table S1. Descriptive statistics (*M*, *SD*) of reaction time (in ms), error proportion (in %), movement distance (in mm), and movement velocity (mm/s) in Study 1.

		Natural optic flow		Inverted optic flow	
Target	Body lean:	Forward	Backward	Forward	Backward
Spider	RT	992 (158)	1009 (156)	995 (168)	1031 (149)
	Error	6.9 (8.8)	4.9 (8.8)	6.0 (8.4)	5.1 (6.4)
	Distance	234 (71)	230 (52)	252 (68)	246 (56)
	Velocity	161 (153)	152 (40)	170 (56)	155 (39)
Flower	RT	1023 (160)	1102 (153)	1021 (151)	1096 (157)
	Error	6.0 (7.0)	5.7 (7.1)	6.2 (10.1)	7.8 (12.2)
	Distance	230 (64)	228 (46)	244 (57)	241 (61)
	Velocity	155 (53)	138 (33)	157 (46)	146 (41)

Table S2. Results of the 2×2×2×2×4 mixed ANOVA of the reaction times.

Table S3. Results of the 2×2×2×2×4 mixed ANOVA of the (log-transformed) error rates.

Movement distance. In the 2×2×2×2×4 mixed ANOVA, the *Target×Body Lean* and the *Target×Body lean×Optic Flow* interaction effects were not significant (both *F*s<1). The *Target×Body lean×Order of SR-mapping, F*(1, 33) = 5.53, *p* = .003, η_p^2=.335, and the five-way interaction effect, *F*(1, 33) = 3.36, *p* = .030, η_p^2=.234, were significant. The main effect of *Target* (larger movements in response to spiders), *F*(1, 33) = 7.15, *p* = .012, η_p^2=.178, and the main effect of *Optic flow* (larger movements in the inverted condition) were also significant, *F*(1, 33) = 7.53, *p* = .010, η_p^2=.186.

Movement velocity. In the 2×2×2×2×4 mixed ANOVA, the *Target×Body Lean* (*F*<1) and the *Target×Body lean×Optic flow* (*F*[1, 33] = 3.03, *p* = .091, η_p^2=.084) interaction effects were not significant. The main effects of *Target* (faster leans in response to spiders), *F*(1, 33) = 63.54,

$p < .001$, $\eta_p^2=.658$; and *Body lean* (faster forward leans) were significant, $F(1, 33) = 14.45$, $p = .001$, $\eta_p^2=.305$.

Spider fear. Five questionnaires had to be excluded due to missing data. Fear of spider sum scores ranged between 0 and 83 (*M*=15.19, *SD*=20.9, Cronbach's α=.957). Exploratory analyses did not show a significant positive correlation with the magnitude of the *Target*×*Body Lean* interaction effect observed in the RT measure (*r*=.04).

Study 2

Table S4. Descriptive statistics (*M*, *SD*) of reaction time (in ms), error proportion (in %), movement distance (in mm), and movement velocity (mm/s) in Study 2.

		Natural optic flow		Inverted optic flow	
Target	Body lean:	Forward	Backward	Forward	Backward
Spider	RT	1187 (124)	1218 (186)	1198 (153)	1252 (145)
	Error	0.3 (1.1)	0.2 (0.8)	1.1 (1.9)	2.1 (5.8)
	Distance	516 (150)	488 (138)	538 (149)	456 (135)
	Velocity	309 (84)	330 (105)	318 (89)	308 (93)
Flower	RT	1195 (160)	1311 (139)	1227 (157)	1349 (157)
	Error	0.3 (1.1)	0.8 (1.6)	0.9 (2.1)	1.8 (3.7)
	Distance	521 (142)	488 (124)	525 (140)	466 (141)
	Velocity	308 (85)	324 (90)	307 (80)	316 (99)

Table S5. Results of the 2×2×2×2×4 mixed ANOVA of the reaction times

Table S6. Results of the 2×2×2×2×4 mixed ANOVA of the (log-transformed) error rates.

Movement distance. The *Target×Body step* (*F*<1) and the *Target×Body step×Optic Flow* (*F*[1, 17] = 1.52, *p* = .235, η_p^2=.082) interaction effects were not significant. The main effects of *Order of optic flow conditions* (larger steps when the inverted condition came first), *F*(1, 17) = 5.10, *p* = .037, η_p^2=.231, *Body step* (larger forward steps), *F*(1, 17) = 25.77, *p* < .001, η_p^2=.603, and the *Body step×Optic flow* interaction effect (larger forward steps and smaller backward steps in the inverted condition than in the natural condition) were significant, *F*(1, 17) = 17.71, *p* = .001, η_p^2=.510.

Movement velocity. In the 2×2×2×2×4 mixed ANOVA, the *Target×Body step* (*F*<1) and the *Target×Body step×Optic flow* (*F*[1, 17] = 2.22, *p*=.154, η_p^2=.116) interaction effects were not significant. The *Body step×Optic flow* interaction (faster backward than forward steps in the natural condition when the natural optic flow condition came first, and vice versa when the inverted condition was first), $F(1, 17) = 9.71$, $p = .006$, $\eta_p^2 = .364$, the *Body step×Optic flow×Order of optic flow condition,* $F(1, 17) = 5.27$, $p = .035$, $\eta_p^2 = .237$, and the *Body step×Optic flow×Order of SR-mapping,* $F(1, 17) = 3.27$, $p = .043$, $\eta_p^2 = .373$, interaction effects were significant. The *Target×Order of SR-mapping,* $F(1, 17) = 3.66$, $p = .034$, $\eta_p^2 = .392$, *Optic flow×Body step* (faster backward than forward step in the natural condition, and vice versa in the inverted condition)*,* $F(1, 17) = 9.71$, $p = .006$, $\eta_p^2 = .364$, *Optic flow×Body Step×Order of optic flow conditions,* $F(1, 17) = 5.27$, $p = .035$, $\eta_p^2 = .237$, and *Optic flow×Body Step×Order of SR-mapping* effects*,* $F(1, 17) = 3.37$, $p = .043$, $\eta_p^2 = .373$, were also significant.

Spider fear. One questionnaire was excluded due to missing data entries. Sum scores ranged between 0 and 69 (M=13.13, SD=19.1, Cronbach's α=.928). Exploratory analyses did not demonstrate a significant positive correlation with the magnitude of the *Target×Body step* interaction effect observed in the RT measure ($r = .375$, $p = .071$).

Study 3

Table S7. Descriptive statistics (*M*, *SD*) of reaction times (in ms), error proportions (in %), movement distance (in mm), and movement velocity (mm/s) in the conditions of Study 3.

		Natural optic flow		Inverted optic flow	
Target	Body step:	Forward	Backward	Forward	Backward
Spider	RT	1246 (163)	1318 (194)	1308 (215)	1415 (236)
	Error	1.5 (3.4)	0.5 (1.7)	1.3 (3.5)	2.8 (5.4)
	Distance	440 (128)	420 (116)	483 (156)	430 (143)
	Velocity	262 (75)	288 (90)	281 (92)	289 (96)
Flower	RT	1269 (161)	1383 (212)	1353 (196)	1459 (243)
	Error	0.5 (1.5)	1.6 (4.2)	3.0 (4.8)	1.4 (2.2)
	Distance	433 (132)	430 (121)	462 (151)	434 (143)
	Velocity	253 (81)	294 (91)	263 (91)	287 (101)
Approach	RT	1418 (169)	—	—	1556 (204)
	Error	2.0 (3.3)	—	—	5.0 (7.8)
Avoidance	RT	—	1319 (157)	1454 (190)	—
	Error	—	2.8 (5.1)	6.7 (7.9)	—

Table S8. Results of the 2×2×2×2×4 mixed ANOVA of the reaction times

Table S9. Results of the 2×2×2×2×4 mixed ANOVA of the (log-transformed) error rates

Movement distance. The *Target×Body step* interaction effect was significant, *F*(1, 24) = 5.41, *p* = .029, η_p^2=.184. Forward steps were larger in response to spiders (*M* = 461 mm, *SE* = 20.8) compared to flowers (*M* = 448 mm, *SE* = 20.1), while backward steps were larger in response to flowers (*M* = 432 mm, *SE* = 19.3) compared to spiders (*M* = 425 mm, *SE* = 19.1). The *Target×Body step×Optic flow* interaction effect was not significant (*F*<1). The main effects of *Order of optic flow conditions* (larger steps when the inverted condition came first), *F*(1, 24) = 7.72, *p*=.010, η_p^2=.243, and *Body step* (larger forward steps), *F*(1, 24) = 8.09, *p*=.009, η_p^2=.252, and the *Body step×Optic flow* interaction effect (larger forward steps in the inverted relative to the natural conditions), $F(1, 24) = 10.68$, $p = .003$, η_p^2=.308, and *Target×Order of optic flow conditions×Order of SR-mappings* interaction effects, $F(1, 24) = 3.41$, p=.034, η_p^2=.299, were also significant.

Movement velocity. The *Target×Body step×Optic flow* interaction was not significant (F<1). The *Target×Body step* interaction was, $F(1, 24) = 8.90$, $p = .006$, η_p^2=.270. Forward steps were executed faster in response to spiders ($M = 0.258$, $SE = 0.013$) than to flowers ($M = 0.272$, $SE = 0.013$), while backward steps were faster in response to spiders ($M = 0.288$, $SE = 0.014$) compared to flowers ($M = 0.290$, $SE = 0.014$). The main effects of *Target* (faster movement execution in response to spiders), $F(1, 24) = 12.14$, $p = .002$, η_p^2=.336; *Body step* (faster backward steps), $F(1, 24) = 21.30$, $p < .001$, η_p^2=.470; *Order of optic flow conditions* (higher movement speed when the inverted condition came first), $F(1, 24) = 4.69$, $p = .040$, η_p^2=.164; the *Target×Optic flow* (faster movements in response to spiders than flowers in the inverted and not in the natural condition), $F(1, 24)$=6.80, p =.015, η_p^2=.221; and the *Body step×Optic flow* interaction effects (faster backward than forward steps in the natural relative to the inverted conditions), $F(1, 24)$= 8.53, p=.007, η_p^2=.262, were also significant.

Spider fear. Two questionnaires had missing data. Fear of spider sum scores ranged between 0 and 43 (M=7.8, SD=10.9, Cronbach's α=.912). Exploratory analyses did not show a moderation by spider fear.

Study 4

Table S10. Descriptive statistics (*M*, *SD*) of reaction times (in ms) and error proportions (in %) in Study 4.

		Natural optic flow		Inverted optic flow	
Target	Body lean:	Forward	Backward	Forward	Backward
Spider	RT	531 (89)	501 (79)	544 (96)	527 (87)
	Error	5.3 (9.0)	3.6 (6.3)	4.8 (4.6)	5.3 (5.8)
Flower	RT	535 (77)	529 (76)	572 (93)	545 (88)
	Error	5.2 (6.6)	5.2 (6.1)	7.3 (6.0)	4.8 (5.7)

Note. Distance and velocity were not analyzed due to the small movement distance of thumbstick movements.

Table S11. Results of the 2×2×2×2×4 mixed ANOVA of the reaction times

Table S12. Results of the 2×2×2×2×4 mixed ANOVA of the (log-transformed) error rates

Spider fear. One questionnaire of Study 2A and Study 2B were excluded due to missing data entries. In Study 2A, sum scores ranged between 0 and 69 (*M*=13.13, *SD*=19.1, Cronbach's α=.928). Exploratory analyses did not demonstrate a significant positive correlation with the magnitude of the observed 2-way interaction effect observed in Study 2A (*r*=.375, *p*=.071). In Study 2B, sum scores varied between 0 and 77 (*M*=14.61, *SD*=18.5, Cronbach's α=.941). Exploratory analyses did not produce a significant positive correlation with the magnitude of the 3-way interaction effect in the RT (*r*=.12, *n.s.*) or error measures (*r*=.02, *n.s.*).

Questionnaires

18 items of the Fear of Spider Questionnaire (Szymanski & O’Donohue, 1995):

1. If I came across a spider now, I would get help from someone else to remove it.
2. Currently, I am sometimes on the look out for spiders.
3. If I saw a spider now, I would think it will harm me.
4. 1 now think a lot about spiders.
5. I would be somewhat afraid to enter a room now, where I have seen a spider before.
6. 1 now would do anything to try to avoid a spider.
7. Currently, I sometimes think about getting bit by a spider.
8. If I encountered a spider now, I wouldn't be able to deal effectively with it.
9. If I encountered a spider now, it would take a long time to get it out of my mind.
10. If I came across a spider now, I would leave the room.
11. If I saw a spider now, I would think it will try to jump on me.
12. If I saw a spider now, 1 would ask someone else to kill it.
13. If I encountered a spider now, I would have images of it trying to get me.
14. If I saw a spider now I would be afraid of it.
15. If I saw a spider now, I would feel very panicky.
16. Spiders are one of my worst fears.
17. I would feel very nervous if I saw a spider now.
18. If I saw a spider now I would probably break out in a sweat and my heart would beat faster.

Post-experimental paper-and-pencil questionnaire:

1. How comfortable was the Oculus headset to wear? (1= very uncomfortable, 7 = very comfortable)

2. Did you experience the visuals from the Oculus headset in general as pleasant or unpleasant? (1= very unpleasant, 7 = very pleasant)
3. Did the visuals cause you physical discomfort (dizziness, nausea, headache etc.)?(yes/no) If yes, which symptoms did you experience? (open answer field)
4. How demanding were the physical activities during the task? (1 = not at all demanding, 7 = very demanding)

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