

Flexible weighting of body-related effects in action production

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Quarterly Journal of Experimental Psychology
2020, Vol. 73(9) 1360–1367
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DOI: 10.1177/1747021820911793
qjep.sagepub.com



Abstract

A previous study on ideomotor action control showed that predictable action effects in the agent's environment influenced how an action is carried out. If participants were required to perform a forceful keypress, they exerted more force when these actions would produce a quiet compared to a loud tone, and this observation suggests that anticipated proprioceptive and auditory action effects are integrated with each other during action planning and control. In light of the typically weak influence of body-related effect found in recent work, we aimed to extend this pattern of results to the intra-modal case of integrating proprioceptive/tactile feedback of a movement and following vibro-tactile effects. Our results suggest that the same weighted integration process as for the cross-modal case applies to the intra-modal case. These observations support the idea of a common mechanism which binds all action-related features in an integrated action representation, irrespective of whether these features relate to efferent or reafferent signals.

Keywords

Ideomotor action; body-related effects; proprioceptive and tactile feedback; action production

Received: 1 April 2019; revised: 7 December 2019; accepted: 28 January 2020

Introduction

Our body is the cornerstone of our actions. It enables us to interact with the environment by our movements, and at the same time, these actions provide sensory feedback. More precisely, our somatosensory system provides us tactile and proprioceptive sensations of our movement, and such sensations further inform about the state of the environment. Even though these sensations unfold only while we carry out an action, anticipations of upcoming sensory changes are functionally relevant already for planning and initiating a body movement (Hommel, 2009; Kunde, 2006; Pfister, 2019; Shin et al., 2010).

Most research on the role of sensory anticipations in action control has focused on auditory or visual modality, whereas recent studies have highlighted that body-related effects (especially tactile and proprioceptive sensations) are recruited in the process just as well (Pfister et al., 2014; Thébault et al., 2018; Wirth et al., 2016; see Pfister, 2019). This notion follows classical formulations of ideomotor theory which maintained that body-related effects (i.e., tactile and proprioceptive effects) are used to represent, select, and control actions (Bain, 1855; Harleß, 1861; Herbart, 1825; James, 1890; Lotze, 1852; see also Stock & Stock,

2004). According to these accounts, humans acquire bidirectional associations between efferent activity and the following sensory changes so that anticipations of desired sensory changes can be used volitionally to re-activate a movement later on. During early ontogeny, these sensory changes mainly comprised body-related sensations, and this type of sensation continues to have a consistent movement-contingent effect throughout the lifespan. Nevertheless, the role of tactile and proprioceptive effects on the physical production of responses has received only limited attention by empirical research to date.

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To examine whether sensory effects are indeed anticipated during action planning and initiation, Kunde (2001) devised a paradigm in which responses triggered predictable visual or auditory effects on a shared dimension (response–effect compatibility). He showed, for instance, that keypress actions were initiated faster in a compatible condition where a tone following the response was of the same intensity (loud tone following a forceful keypress, quiet tone following a soft keypress) compared with an incompatible condition (loud tone following a soft keypress, quiet tone following a forceful keypress). Using the same paradigm, Kunde et al. (2004) found that sensory effects also influence how the movements are executed. In this experiment, the force exerted on the key changed as a function of the upcoming action effects. For instance, for forceful responses, the pressure exerted on the response key was lower if this response was to trigger a loud effect tone than if this response was to trigger a quiet tone.

Kunde et al. (2004) interpreted this impact of anticipated action effects on response execution in light of the extended Paillard–Frasse hypothesis (Aschersleben & Prinz, 1997; Frasse, 1980; Paillard, 1949). This hypothesis has been studied mainly in sensorimotor synchronisation tasks, in which participants are to synchronise finger taps with rhythmic tones. A consistent observation in such tasks is that the finger tap is made slightly (20–50 ms) before the tone rather than in perfect synchrony (Aschersleben & Prinz, 1995; Billon et al., 1996; for reviews, see Aschersleben, 2002; Repp, 2005). To account for this finding, the Paillard–Frasse hypothesis holds that participants aim to synchronise the perceived time of the proprioceptive signals of the movement and the auditory signals relating to the tone. Both signals come with different nerve conduction rates so that slight physical asynchrony is necessary to synchronise the perceptual timing of both events. Crucially, coupling delayed action effects with the participants' taps has a direct and linear effect on the time a tap is produced: the longer the action–effect delay, the earlier the onset of the finger tap (Aschersleben & Prinz, 1997). This suggests that different action-related temporal features are averaged in the corresponding event representation so that the timing of the tapping movement needs to be adjusted to keep the average registered time constant (the extended Paillard–Frasse hypothesis). Kunde et al. (2004) suggested that a similar compensatory averaging process affects the force exerted during action execution: if an agent aims at producing a constant mean intensity, a quiet tone effect calls for a higher intensity of action (i.e., higher peak force [PF]) as a loud tone effect (i.e., lower PF).¹ In a similar vein, Horváth et al. (2018) found that the PF produced during tapping was attenuated by the presence of an auditory effect compared with situations without additional effects.

With the present experiment, we aimed at extending the findings of such a cross-modal averaging process to the

intra-modal interplay of proprioceptive/tactile feedback of a movement and vibro-tactile effects triggered by this movement. Although the interplay between different features is typically stronger or at least equally strong for intra-modal compared with cross-modal settings (e.g., Bjorkman, 1967; Zmigrod et al., 2009), we believe that the interplay of proprioceptive/tactile feedback of a movement and the following vibro-tactile effects is still an important empirical question, because previous studies on the role of such effects in action planning have consistently reported a relatively weak impact of body-related effects (Pfister et al., 2014; Thébault et al., 2018; Wirth et al., 2016; for corresponding observations for the processing of tactile distractors, see Wesslein et al., 2014). This could suggest that body-related effects (here: proprioceptive and tactile events) are less attended—or possibly even suppressed—during action production. Whether the proposed averaging process also takes place intra-modally is thus an open question.

To answer this question, we conducted an experiment built on the set-up of Kunde et al. (2004), but we implemented vibro-tactile rather than auditory action effects. On each trial, our participants thus performed either a forceful or a soft keypress in response to an imperative stimulus, and their keypresses triggered either a high-intensity or a low-intensity vibration. Following Kunde et al. (2004), we measured the PF exerted for each response and probed whether it would vary as a function of the following effect intensity. We supplemented this measure by also assessing response times (RTs) and error rates as measures tapping into the efficiency of action planning and initiation. Here, we expected to observe a response–effect compatibility effect in terms of faster responses when action and effect intensity were compatible compared with when incompatible. In keeping with previous findings on body-related effects, this should be the case especially for the slower end of the RT distribution which we examined by RT distribution analyses (Kunde, 2001; Kunde et al., 2004; Pfister et al., 2014; Thébault et al., 2018; Wirth et al., 2016).

Method

Participants

We recruited 24 participants who gave written informed consent to take part in the experiment (mean age = 23.71 years; 14 females; three left-handed). All participants were naïve about the aim of the experiment. This sample size allowed for a power of $1 - \beta = 0.8$ for effect sizes of $d_z \geq 0.6$ for a repeated-measures design and a two-tailed test at $\alpha = .05$ (computed via the `power.t.test` function of R3.3.0); the effect size for the impact of effect intensity in Kunde et al. (2004) amounted to $d_z = \sqrt{F} / \sqrt{n} = \sqrt{18.72} / \sqrt{16} = 1.08$.

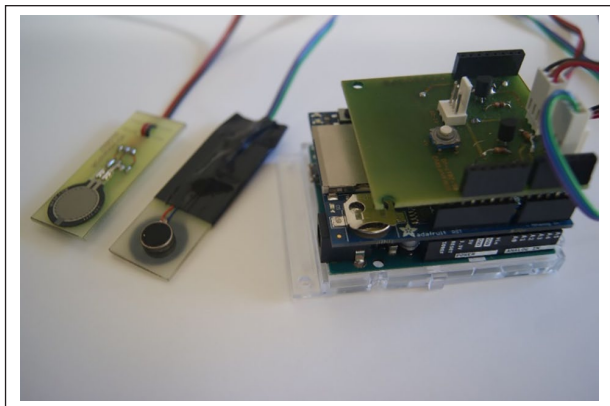


Figure 1. Custom-built keys with a force-sensitive resistor (FSR) and a vibro-motor (on the left) connected to an Arduino interface (on the right).

Material

The experiment was conducted on a computer with a screen size of 15 in. (resolution: 1600×900). The stimuli were two white letters (X and H, Droid Sans Mono, 60 px character height) presented on a black background. Two custom-built keys were used (Figure 1; cf. Thébault et al., 2018). On one side of each key, a force-sensitive resistor (FSR-402 from Interlink Electronics, Santa Barbara, CA, USA) with a round sensing area of 0.5 in. in diameter allowed determining the PF exerted on the keys. On the other side, we installed a vibrating motor like those used in a smartphone. The force-sensitive resistor and the vibrating motor were controlled by an Arduino interface (Arduino Leonardo, Somerville, MA, USA). We used OpenSesame 3.1.9 to perform the experiment (Mathôt et al., 2012).

Procedure

Participants were seated in front of the computer in a quiet room. They held the keys with the thumb and forefinger of each hand. We specified to keep the hands in their respective space (i.e., right hand in the right space, and vice versa). For one target letter (X), participants had to exert a forceful pressure on the key, and for the other target letter (H), they exerted a soft pressure. Half of the participants used the dominant hand for forceful responses and the non-dominant hand for soft responses, whereas the other half used the non-dominant hand for forceful responses and the dominant hand for soft responses. Stimuli were presented for 250 ms and participants had up to 1,500 ms to respond. Each keypress triggered a vibration effect, the intensity of which could be either compatible or incompatible to the intensity of the response; the type of keypress was determined by a threshold according to the intensity of the responses (see the next paragraph for details). The vibrations started 200 ms after the force had reached the

threshold and lasted for 250 ms.² The next trial followed after 1,500 ms.

Response–effect compatibility was manipulated within participants. Participants worked through 10 blocks of 16 trials for each experimental condition for a total of 320 trials. Half of the participants performed the compatible condition first, whereas the other half performed the incompatible condition first. In the compatible condition, a forceful (vs. soft) pressure triggered a high-intensity (vs. low-intensity) vibration, and the reverse was true in the incompatible condition. To avoid vibrations after errors, two thresholds were used; if a forceful response was required, vibrations were only triggered when the applied force exceeded 5.23 N; if a soft response was required, vibrations were already triggered when the applied force exceeded 0.52 N (note that this procedure deviates from Kunde et al., 2004, where the effect of presentation was tied to the PF of the individual trial). So, when a participant pressed softly when a forceful response was required, no vibration was triggered. There was dedicated training phase for the participants, but they were informed during instructions that absent vibrations after the keypress would indicate an error. The frequencies of vibrations were controlled by the Arduino program; values used in the Arduino program were 90 and 200, respectively.

Statistical analysis

Dependent variables were PF, RT, and error rates. PFs were read from the force-sensitive resistor and converted to Newton. The maximum value measured by the force-sensitive resistors was 10 N. Errors of commission were defined as trials in which participants exerted the wrong amount of force (pressing forcefully when a soft keypress was required, and vice versa), whereas errors of omission were defined as trials in which participants did not start to press the key in the response window of 1,500 ms. Two measures of RT were used for the following analyses: The first index (RT1) was the time from stimulus onset until the applied force reached the required threshold, and the second index (RT2) was the time between reaching the threshold and PF. For all RT analyses, responses under 250 ms and above 1500 ms were removed from the statistical analysis; then, of the remaining RTs, and also for PF, we removed those that deviated more than ± 2.5 standard deviations from the corresponding cell mean, computed separately for each participant and experimental condition. These criteria were chosen a priori, based on previous studies.

We analysed the effect of the response type (forceful vs. soft) and vibration intensity (high vs. low) by means of separate 2×2 repeated-measures analyses of variances (ANOVAs) for PF, RT, and error rates. Statistics were performed with JASP (JASP Team, 2019).

Table 1. Mean response times (RT1 and RT2 in milliseconds), error rates (PE, percentage of error in %), and peak forces (PF in Newton) as a function of response type (soft vs. forceful) and vibration intensity of the following effect (low vs. high).

Response	PF		RT1		RT2		PE	
	Vibration intensity		Vibration intensity		Vibration intensity		Vibration intensity	
	Low	High	Low	High	Low	High	Low	High
Soft	4.35	2.43	380	410	357	350	2.87	3.69
Forceful	41.71	33.53	420	418	404	375	6.19	9.32

RT: response time.

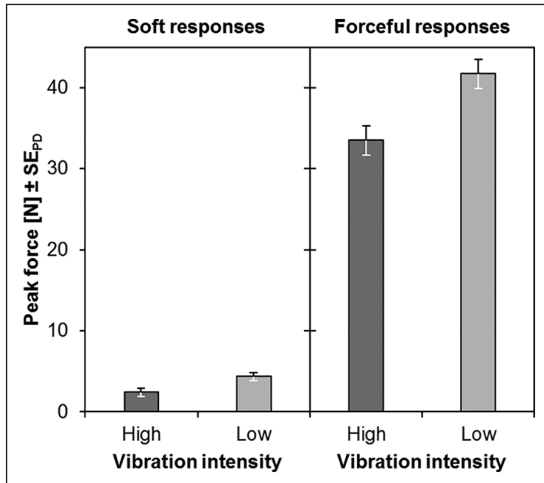


Figure 2. Peak force (in Newton) as a function of response type (forceful vs. soft) and vibration intensity (high vs. low). Error bars represent standard errors of paired differences for the comparison of low- and high-intensity vibrations (Pfister & Janczyk, 2013).

Results

Table 1 shows the descriptive statistics for PF, RT, and error rates. A graphical representation of the percentage of error (PE) data is shown in Figure 2 (see the Supplementary Material for plots of the remaining variables).

PF. A significant main effect of vibration intensity indicated a higher PF for low- compared with high-intensity vibrations, $F(1, 23)=39.34$, $p<.001$, $\eta_p^2=.63$. Not surprisingly, forceful responses also came with a higher PF than soft responses, $F(1, 23)=60.77$, $p<.001$, $\eta_p^2=.73$. An interaction emerged between response type and vibration intensity, $F(1, 23)=9.09$, $p=.006$, $\eta_p^2=.28$, due to a larger impact of vibration intensity on forceful compared with soft responses. These results, similar to those of Kunde et al. (2004), highlight that participants exerted more force when expecting a low-intensity vibration than a high-intensity vibration, and this pattern was more pronounced for forceful than for soft keypresses (see Figure 2).

In addition, we assessed the temporal dynamics of PF for each type of response (i.e., forceful and soft responses)

across the experiment in an exploratory analysis (see Figure 3). The trials of each condition were split into four equally sized blocks (1–20, 21–40, etc.). Analyses were computed by a 2×4 ANOVA to test for the effects of compatibility and block (1–4). This analysis found significant effects of compatibility and block and a significant interaction for both responses ($ps<.010$), whereas simple-effects analyses indicated a robust trend for each block in both responses ($ps<.001$).

RTs. RT1 was longer for forceful responses than for soft responses, $F(1, 23)=8.5$, $p=.008$, $\eta_p^2=.27$, and a main effect of vibration intensity was driven by overall longer RT1 for high-intensity vibrations than for low-intensity vibrations, $F(1, 23)=4.74$, $p=.040$, $\eta_p^2=.17$. The interaction was not significant, $F(1,23)=2.57$, $p=.122$, $\eta_p^2=.1$, although follow-up analyses with a Bayesian repeated-measures ANOVA³ with the same factors—response type (forceful vs. soft) and vibration intensity (high vs. low)—suggested that this effect might be due to a lack of power, $BF_{10}=1.29$. RT2 showed a similar pattern, although only the main effect of response intensity was statistically significant, $F(1, 23)=5.11$, $p=.034$, $\eta_p^2=.18$. The main effect of vibration intensity, $F(1, 23)=3.58$, $p=.071$, $\eta_p^2=.14$, and the interaction, $F(1, 23)=1.24$, $p=.278$, $\eta_p^2=.05$, did not cross the conventional alpha level.

To follow up on the results for RT1, we binned the individual data into separate quintiles for compatible and incompatible action-effect mappings (see Figure 4). A 2×5 ANOVA was used to test the main effects of compatibility and quintile, and their interaction. We found a significant effect of quintile, $F(4, 92)=264.75$, $p<.001$, $\eta_p^2=.92$, but no effect of compatibility and interaction, $F(4, 92)=0.975$, $p=.425$, $\eta_p^2=.04$. As an exploratory analysis, we repeated this procedure for each response type (i.e., forceful and soft responses). For both response types, there was a main effect of bin ($ps<.001$). For forceful responses, we did not observe a further effect of compatibility or an interaction, $F(4, 92)=0.08$, $p=.988$, $\eta_p^2=.003$. For soft responses, we observed a significant effect of compatibility, $F(1, 23)=15.62$, $p<.001$, $\eta_p^2=.40$, and a significant effect of interaction, $F(1, 23)=3.63$, $p=.009$, $\eta_p^2=.14$.

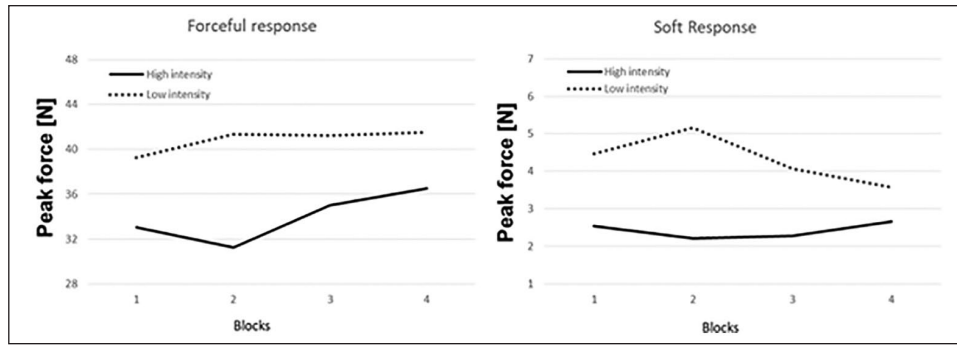


Figure 3. Mean peak forces (in Newton) for forceful responses (left panel) and soft responses (right panel) across the four blocks and high- and low-intensity effects. The first block corresponds to the first 20 responses, the second block to the next 20, and so on. The peak forces were always weaker for high intensity of tactile vibrations than for low intensity of tactile vibrations, although the difference decreases across blocks.

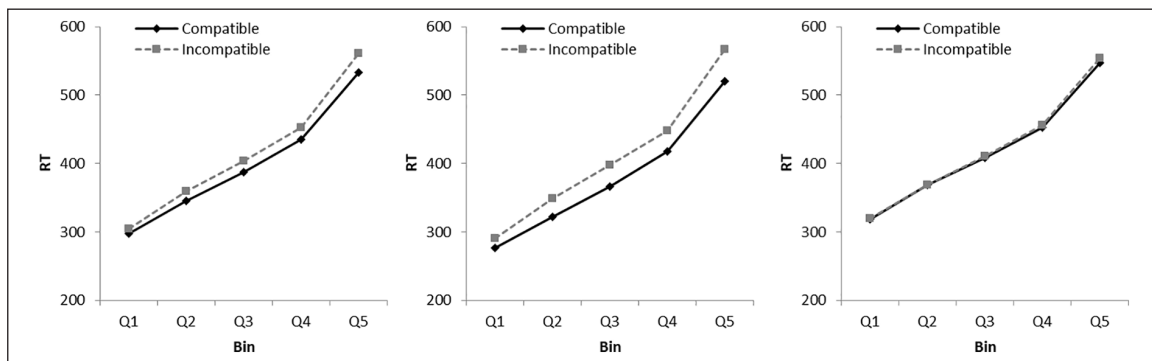


Figure 4. Response time (RT) results of the quintile analysis for all data (left panel), and soft responses (middle panel) and forceful responses (right panel) in compatible and incompatible conditions (measured in milliseconds). Compatible trials include low-intensity vibrations for soft responses and high-intensity vibrations for forceful responses, whereas incompatible trials include the remaining combinations.

Error rates. The mean error rate was 5.52%. There were significant main effects for response intensity, $F(1, 23)=7.94$, $p=.010$, $\eta_p^2=.257$, and vibration intensity, $F(1, 23)=4.76$, $p=.039$, $\eta_p^2=.17$, but no interaction, $F(1, 23)=2.5$, $p=.127$, $\eta_p^2=.09$.

Discussion

This study investigated the anticipation of body-related effects and its impact on how actions are executed. We found that action-contingent vibro-tactile effects do indeed affect the force exerted during action production as demonstrated by the analysis of PF: When actions would trigger a high-intensity vibration, participants pressed more softly than when their actions would trigger a low-intensity vibration. This observation suggests that the hypothesised averaging (i.e., weighted integration) process for different effect types also occurs intra-modally regarding vibro-tactile effects, on the one hand, and proprioceptive and tactile feedback triggered during the movement, on the other hand. We consider this result closely related to the

finding of Kunde et al. (2004) regarding environment-related effects.

As expected, vibro-tactile effects also influenced action selection as suggested by the distribution analysis of the RT data, yielding additional evidence for the involvement of body-related effects in action planning and initiation (see Pfister, 2019; Pfister et al., 2014; Thébault et al., 2018; Wirth et al., 2016). As in previous work, however, the impact of body-related vibro-tactile effects on RT measures was modest, suggesting that such features are not as strongly represented alongside the actual proprioceptive and tactile effects than action effects of different modalities (e.g., visual or auditory effects; see Kunde, 2001, 2003). This explanation likely needs to be supplemented by additional factors, though, because we observed a markedly different pattern for soft and forceful responses, with a detectable influence of response–effect compatibility for soft responses which increase across the RT distribution (see also Pfister et al., 2014; Thébault et al., 2018), whereas there was no sign for forceful responses. Note, however, that our thresholds for determining the RT

differed between the two responses so that force is needed to surpass a much larger threshold for forceful than for soft responses. This technical aspect might have contributed to the consistent absence of RT effects for forceful responses and should be taken into account when designing further studies in the present experimental design. It thus seems safe to assume that the individual features that form an action representation mutually interact, and that they are compiled to feature compounds that result from a (weighted) integration process along any dimension.

A further critical aspect of the present design is that our manipulation of body-related action effects drew on two types of afferent signals: reafferent and exafferent ones. Following Proske and Gandevia (2012), we reserve the term exafference “for afferent signals generated by stimuli of an external origin and the term reafference [. . .] for afferent activity arising from the body’s own action” (p. 1671). Following this definition, in our task, the afferences generated during a response and in its aftermath comprise reafferent signals due to proprioceptive and tactile effects caused by moving the finger, and they comprise exafferent signals due to the vibro-tactile stimulations triggered by each movement. Although the proprioceptive and tactile system are closely entangled (Collins et al., 2005; Gibson, 1962; Yoshioka et al., 2011), both types of body-related effects have a specific function as the former is geared towards processing reafferences, whereas the latter is geared towards processing exafferences (Gapenne, 2014). Our results suggest that both types of afferences are integrated flexibly during action control. This conclusion mirrors phenomenological accounts which stress that experiencing the world with our bodily senses always co-occurs with ourselves experiencing our own bodily sensations (Merleau-Ponty, 1962; Thompson, 2005; see also Legrand, 2007). Following this reasoning, classical distinctions, such as resident versus remote effects (James, 1890), and newer distinctions, such as body-related versus environment-related effects (Pfister, 2019), capture mainly operational differences between different sensory signals while all types of action effects appear to be functionally equivalent (see also Thébault et al., 2018). The relative weight of each (type of) sensory signal, however, seems to be adjusted flexibly during action planning and control.

Finally, the results of our post hoc analysis suggested a systematic temporal evolution of the impact of the vibration effects on the force exerted by the participants. Even though weighting processes seem to be present throughout the experiment—that is, PFs were consistently lower for high vibro-tactile intensity than for low vibro-tactile intensity—the size of this impact diminishes over the course of the experiment. While remaining cautious about these results, this observation might be taken to suggest that different effects of a particular action are attended depending on the current context and the specific task at hand. Arguably, the production of different force levels is a more unusual task than the button-pressing task or the use of

power versus precision grips used in previous work on the integration of different types of action effects (e.g., Camus et al., 2018; Lestage et al., 2018) so that participants might have attended this feature of the action strongly in early stages of each condition. When becoming more familiar with the mechanics of the task, participants might then have shifted their focus more strongly on the vibro-tactile effects of their consequences which would increase their impact on action control. As these effects were nominally task-irrelevant, however, attention might slowly fade back to the task-relevant distinction of forceful and soft key-presses in later stages. Across all stages of the task, however, our study provides a demonstration of the impact of a coupling between proprioceptive and tactile effect and the role of this process for action execution.

At the same time, the study of body-related effects and their role in ideomotor action control still offers many avenues, especially regarding the interplay of such effects with other modalities (see Lestage et al., 2018) and the role of actually perceived rather than anticipated action effects.

Declaration of conflicting interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) received no financial support for the research, authorship, and/or publication of this article.

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Supplementary Material

The Supplementary Material is available at: qjep.sagepub.com

Notes

1. We follow previous work (Kunde et al., 2004) by using the term “averaging” loosely to describe any form of combination and integration. Whether this integration conforms to a strict mathematical average is an open question, with recent observations pointing to a process of weighted integration rather than direct averaging (e.g., Camus, Hommel, Brouillet, & Brunel, 2018; see also Neszemélyi & Horváth, 2017).
2. In this procedure, vibrations may at times commence before the participant has reached the peak force (PF) of a given trial. Parts of the pattern observed in the PF data could therefore be due to experienced rather than anticipated action effects. This potential influence cannot fully explain the observed results, however, as systematic differences in the amount of force exerted were visible already during early stages of the response (i.e., before onset of the vibration).
3. Bayesian analyses used the default JASP Cauchy priors (r scale): fixed effects=0.5, random effects=1, and covariates=0.354 (Rouder, Morey, Speckman, & Province, 2012).

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