



High or low expectations: Expected intensity of action outcome is embedded in action kinetics

Batel Buaron^a, Daniel Reznik^b, Roy Mukamel^{a,*}

^a Sagol School of Neuroscience and School of Psychological Sciences, Tel-Aviv University, Israel

^b Department of Psychology, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

ARTICLE INFO

Keywords:

Action kinetics
Expectation
Press force

ABSTRACT

Goal-directed actions are performed in order to attain certain sensory consequences in the world. However, expected attributes of these consequences can affect the kinetics of the action. In a set of three studies ($n = 120$), we examined how expected attributes of stimulus outcome (intensity) shape the kinetics of the triggering action (applied force), even when the action kinetic and attribute are independent. We show that during action execution (button presses), the expected intensity of sensory outcome affects the applied force of the stimulus-producing action in an inverse fashion. Thus, participants applied more force when the expected intensity of the outcome was low (vs. high intensity outcome). In the absence of expectations or when actions were performed in response to the sensory event, no intensity-dependent force modulations were found. Thus, expectations of stimulus intensity and causality play an important role in shaping action kinetics. Finally, we examined the relationship between kinetics and perception and found no influence of applied force level on perceptual detection of low intensity (near-threshold) outcome stimuli, suggesting no causal link between the two. Taken together, our results demonstrate that action kinetics are embedded with high-level context such as the expectation of consequence intensity and the causal relationship with environmental cues.

1. Introduction

To successfully interact with the world, one must be able to predict the outcome of one's own actions. It is commonly appreciated that the kinetics of a repeated action (e.g., the action's execution force, velocity, trajectory etc.) can be highly variable. Classical motor learning theories mostly attributed such kinetic variability to neural noise or muscle fatigue (e.g., see Schmidt, Lee, Winstein, Wulf, & Zelaznik, 2018). However, recent evidence demonstrates that variability in action kinetics can also be accounted for by higher cognitive and contextual factors such as the goal of the action (Ansuini et al., 2015; Rosenbaum, Chapman, Weigelt, Weiss, & van der Wel, 2012). For example, the kinetics of the simple act of reaching for a glass are different if the subsequent action is to drink or to pour its content (Comalli et al., 2016). Furthermore, it has been shown that human observers are adept at detecting such subtle nuances – allowing them to infer underlying intentions (Cavallo, Koul, Ansuini, Capozzi, & Becchio, 2016).

Not only complex movements (such as reaching) have been shown to be affected by high-level contextual factors, but also simple actions such as pressing a button. For example, participants tend to apply more force

when pressing the same button, depending on whether or not this button is expected to trigger a sound (Cao, Kunde, & Haendel, 2020; Horvath, Biro, & Neszemlyi, 2018). In addition, press force was found to depend on the timing of the sensory feedback, such that participants apply more force on a button as expected delay time between action and auditory outcome increases (Cao, Kunde, et al., 2020; Neszemlyi & Horvath, 2018). Responding to sensory stimuli was also found to affect action force. For example, supplementing a visual cue with a loud auditory tone has been shown to increase applied force relative to the response to a visual cue alone (Anzak, Tan, Pogosyan, & Brown, 2011). Given that most studies only compared the existence of an association (yes/no) of action with sensory consequence, it is unclear whether action kinetics (i. e. press force) are affected by properties of the expected stimulus (e.g. stimulus intensity). Furthermore, while previous studies focused on auditory stimuli, it is still unknown whether differences in press force generalize to other sensory modalities as well.

Despite previous studies showing that context affects action kinetics, the mechanism and functional relevance of this phenomenon is not yet understood. One possible explanation of such outcome-dependent differences in kinetics could represent the encoding of the expected sensory

* Corresponding author.

E-mail address: rmukamel@tauex.tau.ac.il (R. Mukamel).

outcome in the motor system. For example, the forward model (Wolpert & Miall, 1996) suggests that the expected outcome of an action is represented in the motor system, such that when an action is executed an ‘efference copy’ of the expected outcome is sent from motor to sensory regions, modulating the activity in those sensory regions and the perceptual report of the sensory stimulus. Previous studies have shown that neural activity in motor regions can differentiate between identical actions that have different action outcomes (Eisenberg, Shmuelof, Vaadia, & Zohary, 2011; Krasovskiy, Gilron, Yeshurun, & Mukamel, 2014). In addition, the EEG readiness potential, a neural marker of movement preparation, was found to distinguish between button presses with and without expected auditory consequences (Reznik, Simon, & Mukamel, 2018). Such expectation-dependent differential activity in motor regions may in turn result in differences in kinetic features of the executed movement.

Another possible explanation for outcome-dependent force differences could be reafferent information. In other words, it is possible that the temporal contingency between action and consequences alone is sufficient to induce modulations of action kinetics even without prior expectation. It was previously shown that cues with different intensities can modulate the kinetics of an action during its execution (Cao, Kunde et al., 2020; Novembre et al., 2018; Ulrich, Rinckenauer, & Miller, 1998). In the current study, we distinguish between the contribution of prediction and the contribution of reafferent information to the modulations of action kinetics.

In a set of three studies, we address these questions and characterize the link between action kinetics and sensory events, by manipulating the relationship between button presses and sensory events in the auditory, tactile and visual modalities. Specifically, in Study 1 we compared the force trajectories of actions generating low and high intensity sounds using a two-way analysis. In addition, we compared the press force of actions when outcome sound intensity was expected versus random, to differentiate the influence of prior expectations from reafferent sensory information. In Study 2 we further examined the difference in press force between expected outcome intensity in the auditory, tactile and visual

modalities and further compared such force differences when participants responded to (rather than generated) the same stimuli. Finally, in Study 3 we examined whether the amount of applied force affects the perception of sensory outcome. Our results support the notion that properties of predicted sensory outcome are embedded in the kinetics of the stimulus-producing action.

2. Materials and methods

2.1. Participants

Across all three studies, we recruited 136 participants. Data from 16 participants were discarded due to technical problems, leaving a total of 120 participants for analysis (43 males, mean age 25.08, range 18–35 years; *Study 1*: 24 participants, 7 males. Mean age: 25.13, range: 21–33 years; *Study 2*: 72 participants, 29 males. Mean age: 25.33, range: 18–35 years; *Study 3*: 24 participants, 7 males. Mean age: 24.26, range: 20–31 years). All participants were healthy, right-handed (determined by self-report) and had normal hearing and normal or corrected to normal vision. Participants were naïve to the purposes of the study. The study conformed to the guidelines that were approved by the ethical committee in Tel-Aviv University. All participants provided written informed consent to participate in the study and were monetarily compensated for their time.

2.2. Force measuring device

In order to measure the force applied by the participants during button presses, we used force sensors (Honeywell FSA series; force range 0-20 N, sensitivity of 0.035 N) mounted on a response box (see Fig. 1A for device setup). Applying force did not cause any movement (depression) of the sensor, such that pressing the sensor felt like pressing a touchscreen. The sensors were connected to analogue pins on Arduino® mega2560. The force applied to the sensors was measured as a change in the output voltage read from the analogue pins (hgihier

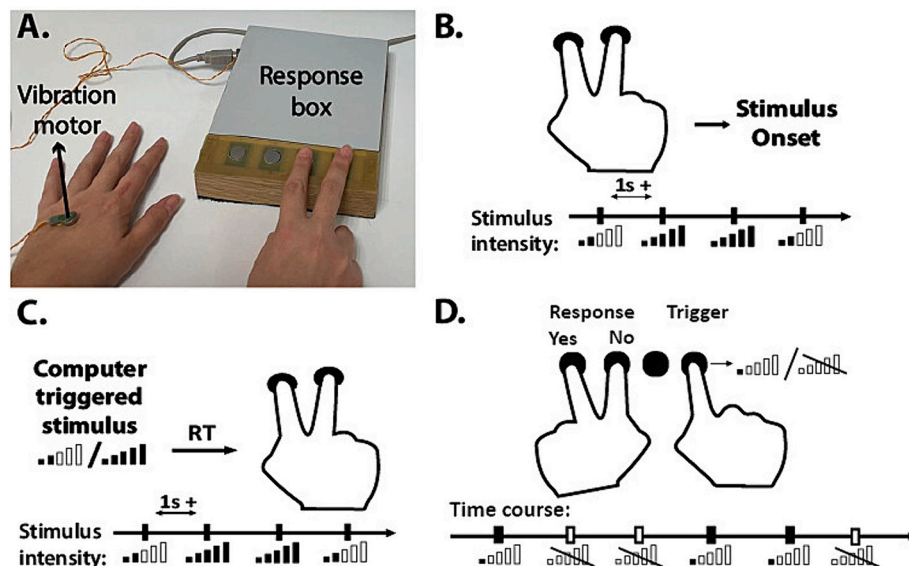


Fig. 1. A. – Force measuring apparatus used in all studies, right-hand finger position relevant to all modalities and conditions in studies 1&2 and vibration motor positioned on left hand (relevant to tactile modality in Study 2 only). B-D: top panels: experimental design bottom panels: experimental timeline. B. – Schematic illustration of experiment design for Expected and Random conditions in Study 1 and Generator condition in Study 2. Participants pressed one of two buttons (free choice) to trigger either a Low or High intensity stimulus. In the Expected (Study 1) and Generator (Study 2) conditions, participants knew in advance which button was coupled with which intensity (mapping was switched between blocks). In the Random condition (Study 1), each button triggered a tone with intensity that randomly varied across trials. C. – Schematic illustration of experiment design for the Follower condition (Study 2). Participants were presented with a stimulus and responded by pressing the corresponding button according to the stimulus intensity. D. – Schematic illustration of experiment design for the detection task (Study 3). Participants pressed a button using their right index finger that either triggered a near-threshold sound or not (random, 50% chance of triggering a sound). Sound detection was reported using one of two buttons with their left hand.

voltage corresponding to higher force levels) and calibrated offline to values in Newton using standard weights (see Fig. S2 in supplementary materials for calibration fit). The voltage from each sensor was read using MATLAB Support Package for Arduino Hardware, at a rate of 60 Hz. This device was used to record press force in all 3 experiments.

2.3. Hardware and software

Sounds were delivered using Creative Sound Blaster Aurora AE-5 sound card and ATH-M30x headphones (Studies 1&2) or E-A-RTONE GOLD inset air pressure earphones (Study 3). The experiment was programmed using Psychtoolbox-3 (version 3.0.16, www.psychtoolbox.org) on MATLAB 2019b (The MathWorks, Inc., Natick, Massachusetts, United States). Visual stimuli were presented using an Nvidia GTX1050TI Graphics card on a 24in screen. Vibrotactile stimulation used for Study 2 was delivered using a Shaftless Vibration Motor (size 10×3.4 mm) controlled by the same Arduino board used for press force data collection.

2.4. Procedure

2.4.1. Study 1

In order to examine the influence of expected stimulus intensity on action kinetics, participants were engaged in a sound-producing task using button-presses with their right hand. Participants were requested to press one of two buttons to trigger a tone using either the index or middle finger (Fig. 1B). Participants were engaged in two different experimental conditions – Expected sound intensity and Random sound intensity conditions. In the Expected sound intensity condition, each button was coupled either with a high or a low intensity auditory stimulus, and participants were aware of this coupling. In order to isolate force modulations that are due to prior expectations from those affected by reafferent sensory information of the evoked stimulus intensity, in a second part of the experiment, participants were requested to press the same two buttons, but on each trial the intensity of the evoked auditory stimulus was either high or low at random (Random sound intensity condition). In other words, in the Random condition participants triggered the auditory stimulus by pressing the same buttons as in the Expected condition but could not predict the outcome intensity. Unbeknownst to participants, we measured their applied force during button presses throughout the experiment. Importantly, in both conditions (Expected and Random), applied force had no effect on stimulus intensity which was fixed – either high (73 dB SPL) or low (23 dB SPL) irrespective of applied force. The auditory stimuli were 300 ms long 1000 Hz pure tones, including a 15 ms up and 15 ms down ramping. The high intensity sound was well within the comfortable range of listening to speech and music (35–90, see Dirks & Kamm, 1976) and the low intensity sound was well above the hearing threshold. At the beginning of the experiment, we verified that participants could hear the low intensity tone and that the high intensity tone was not too loud.

Throughout the experiment, participants were free to choose which button to press in each trial, however they were requested to try and balance their choices between buttons, (i.e., not to prefer one button over the other) and keep the button order as random as possible. Tone was delivered immediately when button-press was detected. In order to avoid potential spill-over effects between trials, we asked participants to keep at least 1 s between consecutive button presses; Trials with shorter inter-press-intervals did not trigger a tone and resulted in an error signal (colour of the fixation on the screen changed to red for 300 ms). Such trials were discarded from further analysis (number of errors per block: Expected condition – $M = 20.63$ range: 3–64; Random condition – $M = 18.79$ range: 0–64) and error trials were replaced with new ones, such that the number of valid trials was 70 for each sound intensity in each block. The experiment consisted of 4 experimental blocks, 2 of each condition (Expected / Random). In the Expected condition, the mapping between each button and sound intensity was fixed in each block and

switched between the first and second block, such that across blocks, each finger (index/middle) was mapped to both sound intensities. This allowed us to compare force levels between sound intensities within the same finger and avoid potential force differences between the fingers. Condition order and intensity mapping within the Expected condition were counter-balanced across participants.

2.4.2. Study 2

In order to examine whether a causal relationship between actions and sensory outcome plays a significant role in the force modulations across expected stimulus intensities, we manipulated the temporal order between actions and sensory events. The experiment included two conditions – Generator and Follower – and was largely similar to the design of Study 1. The Generator condition was identical to the Expected sound intensity condition in Study 1 – participants were instructed to press buttons with known button to stimulus-intensity mappings. In the Follower condition, the temporal order (and causal relationship) between the action and stimuli was reversed. Participants were presented with either a high or low-intensity stimulus (identical to the ones used in the Generator condition) and had to respond by pressing the corresponding button (see Fig. 1C). Participants were requested to respond as accurately as possible with no imposed time constraint. The time interval between responses and initiation of the stimulus in the next trial was 1 s. As in Study 1, each condition consisted of 2 blocks and the mapping between buttons (index/middle finger) and stimulus intensity (low/high intensity either for triggering or responding) was switched across blocks. Each block lasted until at least 70 valid trials in each condition were collected (number of errors per block in the Generator condition, caused by waiting < 1 s between presses – $M = 18.674$ range: 0–87; number of errors in Follower condition, caused by responding the wrong intensity: mean across participants $M = 3.069$ range: 0–20).

In order to examine whether the force modulations found in Study 1 are unique to the auditory modality, we expanded our exploration in this study to the tactile and visual modalities as well. Participants were randomly assigned to one of the three sensory modalities, 24 participants in each modality group, such that in each modality participants completed both the Generator and the Follower conditions. In all groups, stimuli intensities were fixed for all participants. In the auditory group, auditory stimuli were identical to those used in Study 1. In the visual group, visual stimuli were Gabor patches 6° in diameter with a spatial frequency of 6 cycles per degree (cpd) located at the center of the screen. The Gabor patch angle was 45° . The high intensity stimulus had an 80% contrast (luminance level 44.87 cd/m^2), while the low intensity stimulus had an 8% contrast (luminance level 44.11 cd/m^2). Visual stimuli were presented for 100 ms. In the tactile group, tactile stimuli were vibrations (akin to a cellular phone on vibrate mode) delivered to the back of participants' left hand using a vibration motor controlled by an analogue pin on Arduino® mega2560 (same device used for collecting press force data; see Fig. 1A). High intensity vibration had a duty cycle of 0.95, while low intensity vibration had a duty cycle value of 0.42. Vibration stimulation was delivered for 300 ms. Prior to the experiment, we verified that each participant could perceive the low intensity stimulus and that the high intensity stimulus was not aversive to them. Adjustments were made to stimuli if needed, but the difference between low and high intensities was kept constant for all participants.

2.4.3. Study 3

In the third study we focused on the relationship between applied force and perception, examining whether changes in applied force are accompanied by changes in detection of low intensity sounds – thus alluding to a potential functional role. In this study, we examined whether detecting sounds at hearing threshold is associated with the amount of applied force used to trigger the sound. To this end, participants were engaged in a Generator task, but this time sounds were delivered at the individual participant's hearing threshold. Sound detection and applied force were measured.

At the beginning of the study, each participant's hearing threshold was estimated using the '1 step up, 2 steps down' method (Gelfand, 2010), with a step size of 1 dB SPL, as used in our previous studies (Reznik, Guttman, Buaron, Zion-Golumbic, & Mukamel, 2021; Reznik, Henkin, Schadel, & Mukamel, 2014). Auditory stimuli were 300 ms pure 1000 Hz tones created using MATLAB. Each participant went through 4 rounds of threshold estimation. During each round, participants pressed a button using their right index finger to trigger a sound. Using the index and middle fingers of their left hand they reported whether or not they detected a sound. If the participant reported sound detection, on the next trial the sound intensity was lowered by 2 dB. Otherwise, the sound intensity was increased by 1 dB. Each round ended when the participant reported detection at a given intensity twice – and this intensity was set as the detection hearing threshold of that round. Out of the four threshold-estimation rounds, we selected the lowest sound level and verified it by presenting it to participants 10 consecutive times and examining their detection level. Sounds that were detected <4 times were re-examined with a sound level of +1 dB, while sounds that were detected >7 times were re-examined using a sound level of -2 dB. The converged sound intensity was used during the main experiment.

During the main experiment, participants were engaged in a Yes/No detection task in which they had to report whether they heard a sound. In each trial, participants pressed a button that triggered the auditory stimulus in 50% of the trials. 300 ms following sound initiation, participants were presented with the question 'Did you detect a sound?' and had to respond as accurately as possible whether a sound was present or not using their left hand (same positioning as in the threshold detection part; see Fig. 1D). The experiment consisted of 6 blocks, 70 trials each (total of 420 trials across the experiment). Each block included a 50–50 ratio of randomly presented sound/no-sound trials.

2.5. Data analysis

In order to evaluate the applied force for triggering stimuli we computed the sum of force values (force sum) in a given time-window. We used a within-subject Student's *t*-test to compare the force sum between high / low intensity stimuli (Studies 1&2) and between detected and not detected sounds (Study 3). Data were analyzed using JASP

(JASP Team, 2019. Version 0.16.0.0) and corrected for multiple comparisons using FDR correction (Benjamini & Hochberg, 1995). To verify enough trials for statistical comparison of force in Study 3, we excluded participants with <42 trials (20% of total sound trials) in either Hit or Miss trials (see results of Study 3). 9 participants (1 male) were excluded due to this criterion, leaving data from 24 participants for analysis.

3. Results

3.1. Study 1

In this study, participants pressed buttons to trigger either low or high intensity sounds. We examined the differences in force sum between low and high intensity sounds in consecutive 50 ms time windows after press + sound initiation (0-600 ms after press initiation). We performed this analysis separately for the Expected and Random sound intensity conditions. In the Expected condition, in which participants knew in advance which button is associated with which sound intensity, we found a significant difference in applied force between expected low and expected high intensity sounds, such that participants applied more force (larger force sum) when they expected low intensity sound outcome relative to a high intensity sound outcome. This difference was significant for all consecutive 50 ms time windows 0-400 ms after press detection / sound onset (see Fig. 2A for force trajectories and Table 1A for full descriptive data and statistics). In principle it is difficult to dissociate force differences that are related to prior expectation from those related to reafferent feedback of sound intensity. In order to disambiguate these two, we performed the same comparison in the Random condition, in which participants could not build prior expectation of sound intensity based on button identity. We found that in the lack of predictive knowledge, participants also applied more force when the intensity of the action outcome was low. However, this effect started later than in the Expected condition and was significant 100-300 ms after press detection and sound onset (see Fig. 2B for force trajectories and Table 1B for full descriptive data and statistics). No differences in press force were observed in the Random condition at the first 100 ms (For individual participants' differences in press force between sound intensities in Random and Expected conditions see Fig. 2c). Significant

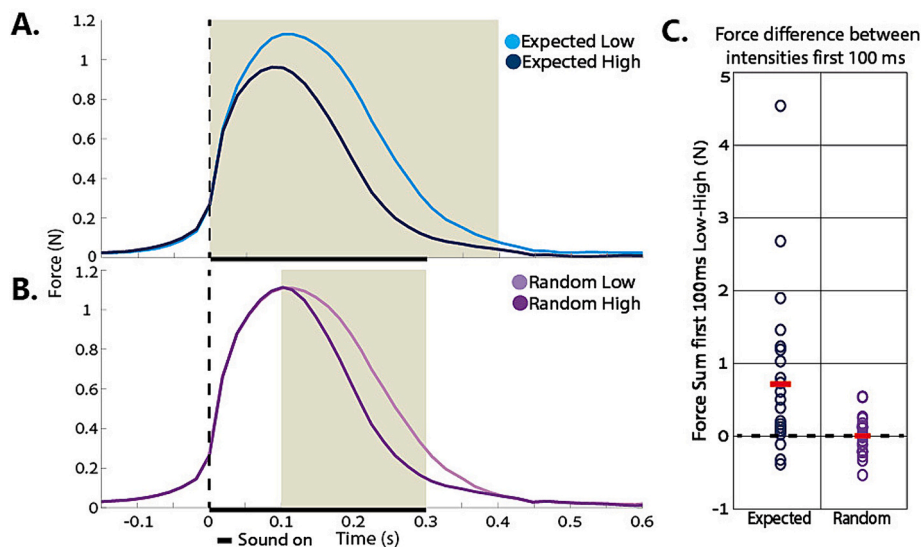


Fig. 2. A + B – Force (Newton) - Time (s) trajectories for triggering Low (light colors) vs. High (dark colors) intensity sounds in the Expected (A) and Random (B) conditions. The dashed line represents press detection + sound onset (time zero). The bold line on the horizontal axis corresponds with sound duration. The shaded background represents time windows in which a significant group difference in force between stimulus intensity conditions was found ($p < 0.05$ FDR corrected). C – Individual participants' differences in force sum between Low and High intensity tones during first 100 ms of button press. Red lines indicate group average, and dashed line at zero represents no difference in force sum between the two sound intensities (Expected condition: $p < 0.001$; Random Condition: $p = 0.92$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Statistical comparison of Force Sum across sound intensities and time windows in the Expected (A; left) and Random (B; right) conditions. Significant differences after correcting for multiple comparisons are marked in bold.

		A. Expected condition (Force Sum)					B. Random condition (Force Sum)																																																																																																																																																																													
Time (ms)	Intensity	Mean (N)	SD	t(23)	p	Mean (N)	SD	t(23)	p																																																																																																																																																																											
0-50 ms	Low	3.993	0.039	2.891	0.008*	4.000	0.039	0.103	0.919																																																																																																																																																																											
	High	3.765	0.037			3.997	0.039				50-100 ms	Low	4.094	0.040	3.220	0.004*	4.052	0.040	0.040	0.969		High	3.607	0.035	4.051	0.040	100-150 ms	Low	3.990	0.039	4.047	0.001*	3.922	0.038	4.194	< 0.001**		High	3.187	0.031	3.697	0.036	150-200 ms	Low	3.486	0.034	4.795	< 0.001**	3.475	0.034	4.777	< 0.001**		High	2.380	0.023	2.761	0.027	200-250 ms	Low	2.604	0.026	5.430	< 0.001**	2.623	0.026	4.119	< 0.001**		High	1.595	0.016	1.841	0.018	250-300 ms	Low	1.754	0.017	5.720	< 0.001**	1.805	0.018	3.052	0.006*		High	1.117	0.011	1.258	0.012	300-350 ms	Low	1.203	0.012	4.229	< 0.001**	1.209	0.012	2.084	0.048		High	0.942	0.009	1.020	0.010	350-400 ms	Low	0.925	0.009	3.044	0.006*	0.894	0.009	0.426	0.674		High	0.816	0.008	0.880	0.009	400-450 ms	Low	0.395	0.004	2.785	0.395	0.386	0.004	1.527	0.140		High	0.316	0.003	0.363	0.004	450-500 ms	Low	0.319	0.003	2.287	0.032	0.317	0.003	1.998	0.058		High	0.268	0.003	0.308	0.003	500-550 ms	Low	0.291	0.003	2.064	0.050	0.289	0.003	1.192	0.245		High	0.241	0.002	0.270	0.003	550-600 ms	Low	0.280	0.003	1.702	0.102	0.272	0.003	1.257	0.221
50-100 ms	Low	4.094	0.040	3.220	0.004*	4.052	0.040	0.040	0.969																																																																																																																																																																											
	High	3.607	0.035			4.051	0.040				100-150 ms	Low	3.990	0.039	4.047	0.001*	3.922	0.038	4.194	< 0.001**		High	3.187	0.031	3.697	0.036	150-200 ms	Low	3.486	0.034	4.795	< 0.001**	3.475	0.034	4.777	< 0.001**		High	2.380	0.023	2.761	0.027	200-250 ms	Low	2.604	0.026	5.430	< 0.001**	2.623	0.026	4.119	< 0.001**		High	1.595	0.016	1.841	0.018	250-300 ms	Low	1.754	0.017	5.720	< 0.001**	1.805	0.018	3.052	0.006*		High	1.117	0.011	1.258	0.012	300-350 ms	Low	1.203	0.012	4.229	< 0.001**	1.209	0.012	2.084	0.048		High	0.942	0.009	1.020	0.010	350-400 ms	Low	0.925	0.009	3.044	0.006*	0.894	0.009	0.426	0.674		High	0.816	0.008	0.880	0.009	400-450 ms	Low	0.395	0.004	2.785	0.395	0.386	0.004	1.527	0.140		High	0.316	0.003	0.363	0.004	450-500 ms	Low	0.319	0.003	2.287	0.032	0.317	0.003	1.998	0.058		High	0.268	0.003	0.308	0.003	500-550 ms	Low	0.291	0.003	2.064	0.050	0.289	0.003	1.192	0.245		High	0.241	0.002	0.270	0.003	550-600 ms	Low	0.280	0.003	1.702	0.102	0.272	0.003	1.257	0.221		High	0.227	0.002	0.240	0.003										
100-150 ms	Low	3.990	0.039	4.047	0.001*	3.922	0.038	4.194	< 0.001**																																																																																																																																																																											
	High	3.187	0.031			3.697	0.036				150-200 ms	Low	3.486	0.034	4.795	< 0.001**	3.475	0.034	4.777	< 0.001**		High	2.380	0.023	2.761	0.027	200-250 ms	Low	2.604	0.026	5.430	< 0.001**	2.623	0.026	4.119	< 0.001**		High	1.595	0.016	1.841	0.018	250-300 ms	Low	1.754	0.017	5.720	< 0.001**	1.805	0.018	3.052	0.006*		High	1.117	0.011	1.258	0.012	300-350 ms	Low	1.203	0.012	4.229	< 0.001**	1.209	0.012	2.084	0.048		High	0.942	0.009	1.020	0.010	350-400 ms	Low	0.925	0.009	3.044	0.006*	0.894	0.009	0.426	0.674		High	0.816	0.008	0.880	0.009	400-450 ms	Low	0.395	0.004	2.785	0.395	0.386	0.004	1.527	0.140		High	0.316	0.003	0.363	0.004	450-500 ms	Low	0.319	0.003	2.287	0.032	0.317	0.003	1.998	0.058		High	0.268	0.003	0.308	0.003	500-550 ms	Low	0.291	0.003	2.064	0.050	0.289	0.003	1.192	0.245		High	0.241	0.002	0.270	0.003	550-600 ms	Low	0.280	0.003	1.702	0.102	0.272	0.003	1.257	0.221		High	0.227	0.002	0.240	0.003																										
150-200 ms	Low	3.486	0.034	4.795	< 0.001**	3.475	0.034	4.777	< 0.001**																																																																																																																																																																											
	High	2.380	0.023			2.761	0.027				200-250 ms	Low	2.604	0.026	5.430	< 0.001**	2.623	0.026	4.119	< 0.001**		High	1.595	0.016	1.841	0.018	250-300 ms	Low	1.754	0.017	5.720	< 0.001**	1.805	0.018	3.052	0.006*		High	1.117	0.011	1.258	0.012	300-350 ms	Low	1.203	0.012	4.229	< 0.001**	1.209	0.012	2.084	0.048		High	0.942	0.009	1.020	0.010	350-400 ms	Low	0.925	0.009	3.044	0.006*	0.894	0.009	0.426	0.674		High	0.816	0.008	0.880	0.009	400-450 ms	Low	0.395	0.004	2.785	0.395	0.386	0.004	1.527	0.140		High	0.316	0.003	0.363	0.004	450-500 ms	Low	0.319	0.003	2.287	0.032	0.317	0.003	1.998	0.058		High	0.268	0.003	0.308	0.003	500-550 ms	Low	0.291	0.003	2.064	0.050	0.289	0.003	1.192	0.245		High	0.241	0.002	0.270	0.003	550-600 ms	Low	0.280	0.003	1.702	0.102	0.272	0.003	1.257	0.221		High	0.227	0.002	0.240	0.003																																										
200-250 ms	Low	2.604	0.026	5.430	< 0.001**	2.623	0.026	4.119	< 0.001**																																																																																																																																																																											
	High	1.595	0.016			1.841	0.018				250-300 ms	Low	1.754	0.017	5.720	< 0.001**	1.805	0.018	3.052	0.006*		High	1.117	0.011	1.258	0.012	300-350 ms	Low	1.203	0.012	4.229	< 0.001**	1.209	0.012	2.084	0.048		High	0.942	0.009	1.020	0.010	350-400 ms	Low	0.925	0.009	3.044	0.006*	0.894	0.009	0.426	0.674		High	0.816	0.008	0.880	0.009	400-450 ms	Low	0.395	0.004	2.785	0.395	0.386	0.004	1.527	0.140		High	0.316	0.003	0.363	0.004	450-500 ms	Low	0.319	0.003	2.287	0.032	0.317	0.003	1.998	0.058		High	0.268	0.003	0.308	0.003	500-550 ms	Low	0.291	0.003	2.064	0.050	0.289	0.003	1.192	0.245		High	0.241	0.002	0.270	0.003	550-600 ms	Low	0.280	0.003	1.702	0.102	0.272	0.003	1.257	0.221		High	0.227	0.002	0.240	0.003																																																										
250-300 ms	Low	1.754	0.017	5.720	< 0.001**	1.805	0.018	3.052	0.006*																																																																																																																																																																											
	High	1.117	0.011			1.258	0.012				300-350 ms	Low	1.203	0.012	4.229	< 0.001**	1.209	0.012	2.084	0.048		High	0.942	0.009	1.020	0.010	350-400 ms	Low	0.925	0.009	3.044	0.006*	0.894	0.009	0.426	0.674		High	0.816	0.008	0.880	0.009	400-450 ms	Low	0.395	0.004	2.785	0.395	0.386	0.004	1.527	0.140		High	0.316	0.003	0.363	0.004	450-500 ms	Low	0.319	0.003	2.287	0.032	0.317	0.003	1.998	0.058		High	0.268	0.003	0.308	0.003	500-550 ms	Low	0.291	0.003	2.064	0.050	0.289	0.003	1.192	0.245		High	0.241	0.002	0.270	0.003	550-600 ms	Low	0.280	0.003	1.702	0.102	0.272	0.003	1.257	0.221		High	0.227	0.002	0.240	0.003																																																																										
300-350 ms	Low	1.203	0.012	4.229	< 0.001**	1.209	0.012	2.084	0.048																																																																																																																																																																											
	High	0.942	0.009			1.020	0.010				350-400 ms	Low	0.925	0.009	3.044	0.006*	0.894	0.009	0.426	0.674		High	0.816	0.008	0.880	0.009	400-450 ms	Low	0.395	0.004	2.785	0.395	0.386	0.004	1.527	0.140		High	0.316	0.003	0.363	0.004	450-500 ms	Low	0.319	0.003	2.287	0.032	0.317	0.003	1.998	0.058		High	0.268	0.003	0.308	0.003	500-550 ms	Low	0.291	0.003	2.064	0.050	0.289	0.003	1.192	0.245		High	0.241	0.002	0.270	0.003	550-600 ms	Low	0.280	0.003	1.702	0.102	0.272	0.003	1.257	0.221		High	0.227	0.002	0.240	0.003																																																																																										
350-400 ms	Low	0.925	0.009	3.044	0.006*	0.894	0.009	0.426	0.674																																																																																																																																																																											
	High	0.816	0.008			0.880	0.009				400-450 ms	Low	0.395	0.004	2.785	0.395	0.386	0.004	1.527	0.140		High	0.316	0.003	0.363	0.004	450-500 ms	Low	0.319	0.003	2.287	0.032	0.317	0.003	1.998	0.058		High	0.268	0.003	0.308	0.003	500-550 ms	Low	0.291	0.003	2.064	0.050	0.289	0.003	1.192	0.245		High	0.241	0.002	0.270	0.003	550-600 ms	Low	0.280	0.003	1.702	0.102	0.272	0.003	1.257	0.221		High	0.227	0.002	0.240	0.003																																																																																																										
400-450 ms	Low	0.395	0.004	2.785	0.395	0.386	0.004	1.527	0.140																																																																																																																																																																											
	High	0.316	0.003			0.363	0.004				450-500 ms	Low	0.319	0.003	2.287	0.032	0.317	0.003	1.998	0.058		High	0.268	0.003	0.308	0.003	500-550 ms	Low	0.291	0.003	2.064	0.050	0.289	0.003	1.192	0.245		High	0.241	0.002	0.270	0.003	550-600 ms	Low	0.280	0.003	1.702	0.102	0.272	0.003	1.257	0.221		High	0.227	0.002	0.240	0.003																																																																																																																										
450-500 ms	Low	0.319	0.003	2.287	0.032	0.317	0.003	1.998	0.058																																																																																																																																																																											
	High	0.268	0.003			0.308	0.003				500-550 ms	Low	0.291	0.003	2.064	0.050	0.289	0.003	1.192	0.245		High	0.241	0.002	0.270	0.003	550-600 ms	Low	0.280	0.003	1.702	0.102	0.272	0.003	1.257	0.221		High	0.227	0.002	0.240	0.003																																																																																																																																										
500-550 ms	Low	0.291	0.003	2.064	0.050	0.289	0.003	1.192	0.245																																																																																																																																																																											
	High	0.241	0.002			0.270	0.003				550-600 ms	Low	0.280	0.003	1.702	0.102	0.272	0.003	1.257	0.221		High	0.227	0.002	0.240	0.003																																																																																																																																																										
550-600 ms	Low	0.280	0.003	1.702	0.102	0.272	0.003	1.257	0.221																																																																																																																																																																											
	High	0.227	0.002			0.240	0.003																																																																																																																																																																													

differences after 100 ms in the Random condition are probably due to sensitivity to the intensity of the auditory feedback and cannot be explained by prior expectations since evoked stimulus intensity was not known in advance. Conversely, early differences in force (<100 ms from press onset) in the Expected condition (that are absent in the Random condition) are most likely related to the expected intensity of sound outcome. Since the aim of our study was to examine the relationship between actions and expected sensory outcome, and in order to avoid potential differences due to reafferent processing, in subsequent studies we focused our analyses only on the time window between 0 and 100 ms. By doing so we avoided as much as possible potential contamination of effects by reafferent feedback signals. Given the results from this study, in the subsequent studies we continued to use the same sample size.

3.2. Study 2

In order to further establish whether the differences in applied forces we found in Study 1 are related to expected intensity of action outcome, we manipulated the causal relationship (temporal order) between action and sensory events. Participants either pressed a button to trigger a sensory event (Generator condition) or pressed a button in response to a sensory event (Follower condition). Sensory events were either auditory, tactile or visual (see methods). Based on the results from Study 1, we focused on sum force data from the time window between 0 and 100 ms after press onset and compared the force sum in this time window between low and high intensity stimuli for each condition (Generator / Follower) and modality (Auditory / Tactile / Visual). We focused on this time window in order to examine the influence of expectations about stimulus intensity on applied force and avoid potential influence of reafferent information (see results of Study 1 for full details).

First, we performed a 2×2 repeated measures ANOVA with condition (Generator / Follower) and stimulus intensity (Low / High) as within-subjects factors, in order to compare applied force between triggering and responding to low and high intensity stimuli, irrespective of stimulus modality. We found a significant difference between conditions, such that participants applied more force in the Follower condition ($M = 11.59$ $SD = 8.61$ N) relative to the Generator condition ($M = 5.45$ $SD = 3.39$ N; $F(1,71) = 55.29$ $p < 0.001$). We found a marginally

significant effect of stimulus intensity, such that participants showed a tendency to apply more force to trigger a low intensity stimulus ($M = 8.62$ $SD = 7.25$ N) relative to a high intensity stimulus ($M = 8.41$ $SD = 7.21$ N; $F(1,71) = 3.51$ $p = 0.065$). We also found a significant interaction effect between condition and stimulus intensity ($F = 4.44$, $p = 0.039$). Post-hoc test revealed that in the Generator condition there was a significant difference between low ($M = 5.65$ $SD = 3.59$ N) and high intensity stimuli ($M = 5.24$ $SD = 3.16$ N; $t(71) = 4.47$ $p < 0.001$), but there was no such difference in the Follower condition (Low intensity stimuli: $M = 11.60$ $SD = 8.63$ N; High intensity stimuli: $M = 11.58$ $SD = 8.60$ N; $t(71) = 0.11$ $p = 0.91$; See Fig. 3A for full force trajectories). Note that this lack of difference is not due to a ceiling effect in the Follower condition, since the dynamic range of our sensor was up to 20 N, with similar sensitivity across the range examined in the current study (see supplement fig. S2).

Next, we examined the difference in applied force between low and high intensity stimuli within each modality separately. To this end, we used two-tailed paired sample Student's t -test, comparing directly between Force Sum for triggering Low and High stimulus intensities within each modality and condition. Results from the Generator condition in the **Auditory** modality replicated the results from Study 1, demonstrating a significant difference in applied force between Low (Force Sum $M = 6.17$ $SD = 4.42$ N) and High intensity auditory stimuli (Force Sum $M = 5.30$ $SD = 3.55$ N; $t(23) = 3.94$ $p < 0.001$). Similarly, in the **Tactile** modality, we found a significant difference in applied force between Low ($M = 6.21$ $SD = 3.73$ N) and High intensity tactile stimuli ($M = 5.92$ $SD = 3.55$ N; $t(23) = 3.22$ $p = 0.004$). In the **Visual** modality we did not find a significant difference between stimulus intensities (Low intensity Force Sum $M = 4.57$ $SD = 1.89$ N; High intensity Force Sum $M = 4.52$ $SD = 1.95$ N; $t(23) = 0.83$; $p = 0.42$; see Fig. 3B). This pattern of results persists after applying correction for multiple comparisons. In the Follower condition, no significant differences between Low and High stimulus intensities were found across all three modalities (**Auditory**: Low intensity $M = 13.99$ $SD = 10.00$ N; High intensity $M = 13.50$ $SD = 9.35$ N; $t(23) = 1.57$ $p = 0.13$; **Tactile**: Low intensity $M = 12.77$ $SD = 6.80$ N; High intensity $M = 12.90$ $SD = 7.12$ N; $t(23) = 0.31$ $p = 0.76$; **Visual**: Low intensity $M = 8.03$ $SD = 7.57$ N; High intensity - $M = 8.34$ $SD = 8.24$ N; $t(23) = 1.64$ $p = 0.11$; see Fig. 3C). Taken together, these results indicate that expected stimulus intensity modulates the force

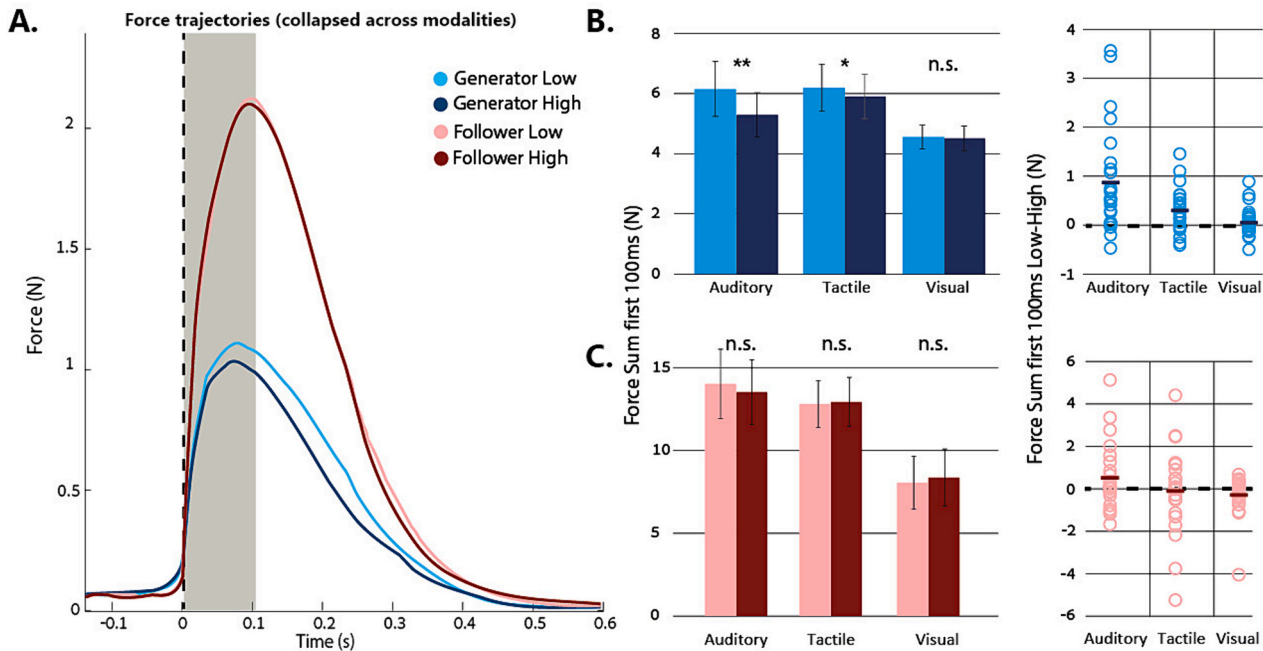


Fig. 3. A – Force trajectories for triggering Low (light colors) and High (dark colors) intensity stimuli in the Generator (blue) and Follower (red) conditions. Dashed line represents press detection time (which is also stimulus onset in the Generator condition). Grayed time window marks the first 100 ms used for analysis. B – Left panel: group mean Force Sum in the 0–100 ms time window in the Generator condition, marked separately for each modality. ** $p < 0.001$, * $p < 0.05$. Right panel: individual participants' differences in applied force between low and high intensity stimuli. Solid lines represent group mean difference. Dashed line at zero represents no difference in force sum between the two stimulus intensities. C – Same as B for the Follower condition. Note the differences in scale between the left panels in B and C (also evident in the trajectories shown in panel A). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

participants implicitly apply when there is a causal relationship between the action and the stimulus. Such pattern of results is not observed when the causal relationship is reversed. This intensity-dependent effect on force in the generator condition is prominent in the auditory and tactile modalities but is absent in the visual modality. In the supplementary materials we present the results of an additional study in the visual domain in which we manipulated another visual feature of actions' visual outcome (stimulus speed; Slow/Fast), and found no modulation of press force either (see supplementary material for full details).

Finally, we also compared the reaction time (RT) for responding to different intensity stimuli in the Follower condition. Collapsing across all modalities, participants tend to respond slower to low intensity stimuli ($M = 882.18$ ms $SD = 200.60$ ms) than to high intensity stimuli ($M = 819.59$ ms $SD = 204.34$ ms; $t(71) = 4.78$ $p < 0.001$). Further examining this separately in each modality, we found such effect in the Auditory (Low intensity: $M = 893.36$ ms $SD = 182.67$ ms; High intensity: $M = 795.17$ ms $SD = 157.26$ ms; $t(23) = 4.21$ $p < 0.001$) and Tactile (Low intensity: $M = 941.95$ ms $SD = 186.99$ ms; High intensity: $M = 883.55$ ms $SD = 149.76$ ms; $t(23) = 4.14$ $p < 0.001$) modalities, but no difference in RT was found in the Visual modality (Low intensity: $M = 811.24$ ms $SD = 208.93$ ms; High intensity: $M = 780.05$ ms $SD = 268.05$ ms; $t(23) = 1.14$ $p = 0.26$).

3.3. Study 3

Studies 1 & 2 point to differences in applied force that depend on the expected intensity of sensory outcome. In order to examine whether applied force affects the perception of the sensory outcome, we used an auditory detection task (see Methods) and focused on the force sum values in the time window between 0 and 100 ms of sound triggering presses. We used a median split to obtain soft / strong press trials (above / below median) and compared the signal detection theory parameters (d' and criterion values) between strong and soft presses using a within-subjects Student's t -test. We calculated the signal detection parameters

as explained in Stanislaw and Todorov (1999). To avoid division by zero, participants with no False Alarms were assigned false alarm probability of $0.5/n$ where n is the number of trials. In addition, we used a Bayesian analysis to evaluate the probability of the null hypothesis for all the performed t -tests.

Compatible with our hearing threshold estimation, participants correctly reported sound detection in 52.5% of the trials in which a sound was actually generated by the button press (range across participants: 21.9%–78.5%; Hit trials). From the trials in which button-presses did not generate a sound, the average proportion of detection reports (i.e. False Alarms) across participants was 6.1% (range: 0%–37.6%). Force Sum values of the first 100 ms of the press were split to soft and strong presses (Below median force (Soft Presses): $M = 2.749$ $SD = 1.693$ N; Above median force (Strong Presses): $M = 5.354$ $SD = 3.016$ N). For each force level separately, we calculated the sensitivity in detecting a near-threshold sound (d') and the tendency to report sound detection (criterion). Comparing the d' measures across force levels did not yield significant differences between presses below median Force Sum level ($M = 1.932$ $SD = 0.141$) and presses above median Force Sum ($M = 1.958$ $SD = 0.154$ z; $t(23) = 0.290$ $p = 0.774$; $BF_{01} = 4.48$). Similar pattern of results was found for the criterion, with no differences between presses below median Force Sum level ($M = 0.891$ $SD = 0.089$ z) and presses above median Force Sum ($M = 0.915$ $SD = 0.089$ z; $t(23) = 0.411$ $p = 0.685$; $BF_{01} = 4.31$; see Fig. 4A).

Next, we directly compared the Force Sum in the first 100 ms of button press between Hit and Miss trials (i.e. all trials in which the button-press generated a sound). No significant difference in applied force was found between Hit ($M = 4.020$ N $SD = 2.491$ N) and Miss trials ($M = 4.017$ N $SD = 2.255$ N; $t(23) = 0.025$ $p = 0.980$; $BF_{01} = 4.66$; see Fig. 4B for full force trajectory and Fig. 4C for mean and individual participants' data). Taken together, all our analyses point to no significant relationship between applied force level and sound detection.

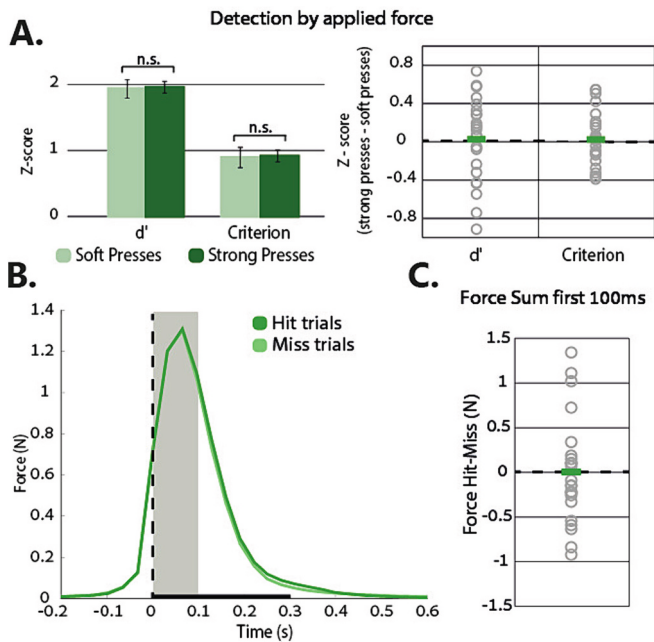


Fig. 4. A. – Left panel: average and SEM d' and criterion values for presses with applied force levels below (Soft) and above (Strong) median during the first 100 ms of press. Right panel: individual participants' difference in d' and criterion between Strong and Soft presses (dots). Green lines represent group mean. Dashed line at zero represents equal parameter value for both levels of applied force. B. – Force trajectories for trials in which button-presses generated a sound separated by Hit or Miss responses. Dashed line represents press detection + sound onset. Grayed time window marks the first 100 ms used for analysis. Bold line on x-axis represents sound duration. C. – Individual participants' differences in press force between Hit and Miss trials. Green line represents group mean difference, and dashed line at zero represents equal force applied between conditions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

In the current study, we examined how action kinetics are affected by the properties of their coupled sensory events. To this end, we measured the force levels participants apply during button presses while manipulating the buttons' relation with sensory stimuli. We found that participants applied higher force levels when pressing a button in order to trigger a low (vs. high) intensity stimulus. We further manipulated the predictability of the outcome and the causal relationship between the action and the stimulus to evaluate their influence on press force. We found that prior expectation of stimulus intensity affects press force immediately from the onset of the action, while presses with no prior expectation started to show a difference in press force only 100 ms after action onset. Furthermore, when actions followed the sensory event (i.e. no causal relationship between action and stimulus), intensity-dependent differences in force levels were abolished. Finally, we found that detection of low intensity outcome stimuli was not influenced by applied force levels, suggesting no significant functional role of force in successful detection of action outcome.

4.1. Expected intensity of action-outcome affects applied force levels

In both studies 1 and 2, we found an inverse relationship between the expected intensity of action consequences and applied force, such that the expectation of low intensity outcome corresponds with higher force levels. Furthermore, when button presses were not associated with expectation of an outcome (as in the 'Follower' condition in experiment 2 in which button presses did not produce an outcome), we found that participants applied the highest amount of force. Interestingly, previous

studies that manipulated the existence (yes/no) of auditory outcome, rather than expectation of outcome property (intensity) report a compatible phenomenon. Participants apply less force when a button is associated with an auditory consequence and more force when the same button press was silent (Cao, Kunde, et al., 2020). This phenomenon is not specific to button presses but generalizes to other actions, such as pinches and taps (Horvath et al., 2018; Neszmelyi & Horvath, 2017). Taken together, these results point to a graded relationship between the expected intensity of auditory outcome (no outcome/low-intensity/high-intensity) and implicit force applied. The lower the expected intensity of sensory outcome, the higher the applied force.

Previous studies examining the relationship between press force and outcome focused mainly on the auditory domain (Cao, Kunde, et al., 2020; Horvath et al., 2018; Neszmelyi & Horvath, 2017, 2018), without examining whether this association generalizes to other modalities, potentially pointing to a fundamental motor mechanism. In our second study, we further examined such relation in the tactile and visual modalities. We found force differences between generating different stimulus intensities only in the auditory and tactile modalities, while it was absent in the visual modality. Lack of differences in the visual modality also persisted when examining different aspects of the visual stimuli (speed; see supplement materials). While it is plausible that in the visual modality applied force levels encode a different parameter from contrast/speed that was not examined in the current study, our results support a functional difference in action-outcome integration in the visual vs. the tactile and auditory modalities. Indications for the uniqueness of such integration in the visual modality can also be found in other sensory-motor paradigms. For example, in the tactile and auditory modality, it is established that self-triggered sensory stimuli are perceived as less intense relative to identical stimuli generated externally (sensory attenuation; Blakemore, Frith, & Wolpert, 1999; Kilteni & Ehrsson, 2017; Weiss, Herwig, & Schutz-Bosbach, 2011; Weiss & Schutz-Bosbach, 2012). However, in the visual modality there is relatively little consensus about the directionality of such effects (Buaron, Reznik, Gilron, & Mukamel, 2020), with some reporting an attenuation of self-triggered visual stimuli (Cardoso-Leite, Mamassian, Schutz-Bosbach, & Waszak, 2010; Dewey & Carr, 2013) while others report an enhancement of such stimuli (Desantis, Roussel, & Waszak, 2014; van Kemenade, Arikian, Kircher, & Straube, 2016). This might be a reflection of a closer association between motor and auditory/tactile modalities relative to the visual modality. Further study is needed in order to understand such differences in action-outcome integration across modalities.

4.2. Level of applied force depends on foreknowledge about the intensity of sensory outcome

When requesting participants to press a button to trigger a sensory stimulus, press-duration is sufficiently long (~400 ms) to be affected by both expectation processes and reafferent processing of perceived stimulus intensity. Previous studies have shown that reafferent information can affect the amount of applied force (Cao, Kunde, et al., 2020; Novembre et al., 2018). Compatible with these results, in Study 1 we show that in a Random condition, in which participants could not build an expectation of the action outcome intensity in advance, we found intensity-dependent modulations only 100 ms after press initiation – presumably due to reafferent feedback. Therefore, in our analysis we focused on the first 100 ms in which any force differences across conditions are more likely to be associated with motor planning and not contaminated by feedback. This time frame for reafferent information is compatible with previous results, suggesting it takes reafferent information ~70 ms to affect action force (Cao, Kunde, et al., 2020). Interestingly, the magnitude of applied force during the first 100 ms in the Random condition was similar to the force used for triggering low intensity sounds in the Expected condition. This suggests that in case of uncertainty, participants behave as if they expect low intensity sound.

To further examine whether the force modulations are due to

expectation of sensory outcome intensity, rather than an association between stimulus intensity and actions, in our second study we manipulated the temporal order between the action and the sensory event. Since expectations are associated with future events, intensity-dependent force-modulations should not be found when the stimulus precedes the action. We found that the initial level of applied force (first 100 ms of action) is not sensitive to stimulus intensity when the stimulus precedes the action, but only when the action is used to generate the stimulus. Note that the lack of difference in the Follower condition is not likely to be explained by a ceiling effect of press force. We measured a maximum force of ~ 2.3 N applied in the Follower condition, compatible with previous studies showing that finger press force can be over 3 N in some conditions (Cao, Kunde, et al., 2020; Neszmelyi & Horvath, 2018). This is well within the range of our force sensitive sensors, which are capable of measuring up to 20 N. The lack of differences between force intensities in the Follower condition is not in agreement with a previous study that shows an increase in press force when responding to higher intensity stimuli (Ulrich et al., 1998). In this study, Ulrich et al. (1998) asked participants to make a speeded reaction towards a tone delivered in 3 different intensities and showed increased force levels when responding to higher intensity sounds. However, unlike in the current study, the task was to respond to the sounds as fast as possible regardless of sound intensity (speeded response). In the current study, sound intensity was integral to the task (2AFC), which required reporting the intensity of the stimulus, rendering accuracy more important than speed. Our results indicate that in such a task, participants apply similar force levels across stimulus intensities.

4.3. Functional role of force modulation

Results from Studies 1 and 2 demonstrate an inverse relationship between expected stimulus intensity and applied force levels – with participants applying higher force levels when the expected outcome intensity was low. Although our low intensity stimuli were well above perceptual thresholds, and participants could detect them in all of the trials, this finding raises a possible functional connection between force and perception – suggesting that participants might be applying higher force levels to facilitate perception. Previous studies have shown that perception of low intensity sounds is enhanced when those sounds are self-triggered (Reznik et al., 2014; Reznik et al., 2021; Reznik, Henkin, Levy, & Mukamel, 2015). Therefore, in our third study, we used a sound-detection task to examine the relationship between applied force and detection but found no correspondence between the two measures. This is in agreement with another study that examined whether applied force levels affect auditory discrimination, using a comparison (rather than detection) paradigm (Endo et al., 2021). In this study, participants had to press buttons at three different pre-determined force levels and their auditory discrimination was measured. They found that discrimination performance was invariant to applied force levels. Taken together, at least with respect to perception, applied force does not seem to play a significant functional role.

A possible explanation for increasing the amount of applied force when expecting low intensity action outcome may come from the way we naturally interact with objects. For example, clapping your hands stronger against each other elicits stronger sounds and creates stronger tactile sensations compared with clapping the hands gently. It is plausible that when low intensity feedback is expected, we automatically increase the vigor of our actions to increase feedback intensity (as happens under natural circumstances), even in cases in which it is known that vigor has no effect on outcome intensity. Another possible explanation for outcome-intensity dependent force modulations was presented by Kunde, Koch, and Hoffmann (2004), who suggested that when performing an action, we aim to have an “average” amount of sensory feedback, therefore actions with lower outcome intensity in one modality will be compensated by increased feedback in another modality. In our case, higher press force results in increased feedback in the

tactile modality. Whether or not force modulations have a functional benefit or are simply an epiphenomenon related to neural processes related to expected sensory outcome remains to be determined.

Another potential explanation, presented by Neszmelyi and Horvath (2018), suggests that applied force is inversely related to the degree of agentic association between action and outcome. In their study, the authors used a similar task to our ‘Generator’ condition but introduced temporal delays between the action and auditory outcome. They report increasing force levels with increasing temporal delays, reaching plateau ~ 200 ms at which delay the applied force levels were similar to those applied when the button press did not produce a sound (silent condition) (Neszmelyi & Horvath, 2018). Although agency was not explicitly probed, it is possible that increasing the temporal delay between action and consequences diminishes the feeling of agency over the sound and after 200 ms such binding is lost. The link between agency and press force is further supported by the intentional binding task (Haggard, 2017), showing that stronger presses are associated with weaker measures of agency (Cao, Steinborn, Kunde, & Haendel, 2020). Taken together, these results suggest that press force might be associated with the binding between action and consequence and therefore associated with different levels of agency. While we did not have agency related measures in our studies, it would be interesting to examine whether participants experience lower levels of agency towards lower (vs. higher) intensity stimuli, and whether such levels of agency could be correlated with the level of applied force.

5. Conclusion

Action kinetics are a rich measure which is influenced by various high-level cognitive constructs such as intentions and future goals. Our results show that properties of the expected sensory outcome are also embedded in subtle kinetic features of the action, such as applied force that are unrelated to the task and can be observed even in a simple action of pressing a button. Thus, by measuring subtle differences in kinetics one can infer the degree of motor-sensory integration. Such a phenomenon can be utilized in future studies as a marker for expectation and also provide a behavioral window into the neural circuits guiding behavior. Our results further show that variability in action could include representation of information about the agent and their state and not just “noise” as was previously suggested (Schmidt et al., 2018). This suggests that models of motor control and sensory-motor integration should consider adding factors representing outcome expectation, sensory reafferent information and causality. Finally, our results also contribute to the field of action and perception, showing that even though expectations of sensory events affect the kinetics of an action, action kinetics does not affect perception of sensory stimuli. This finding enriches our understanding of the interplay between motor and sensory regions, suggesting that while the motor system sends signals to sensory regions about upcoming action consequence (Wolpert & Miall, 1996), those signals are not likely to include information about the kinetics of the action itself.

CRediT authorship contribution statement

Batel Buaron: Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Daniel Reznik:** Writing – original draft, Methodology, Conceptualization. **Roy Mukamel:** Writing – original draft, Supervision, Methodology, Funding acquisition, Conceptualization.

Data availability

Data from all participants of each study can be found in: <https://data.mendeley.com/datasets/vkrjtbyh2m/2>

Acknowledgements

The study was supported by the Israel Science Foundation (grant No. 2392/19 to R.M.). The authors thank lab members for constructive comments and fruitful suggestions.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cognition.2024.105887>.

References

- Ansuini, C., Cavallo, A., Koul, A., Jacono, M., Yang, Y., & Becchio, C. (2015). Predicting object size from hand kinematics: A temporal perspective. *PLoS One*, *10*(3), Article e0120432.
- Anzak, A., Tan, H., Pogossyan, A., & Brown, P. (2011). Doing better than your best: Loud auditory stimulation yields improvements in maximal voluntary force. *Experimental Brain Research*, *208*(2), 237–243.
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal statistical society: series B (Methodological)*, *57*(1), 289–300.
- Blakemore, S. J., Frith, C. D., & Wolpert, D. M. (1999). Spatio-temporal prediction modulates the perception of self-produced stimuli. *Journal of Cognitive Neuroscience*, *11*(5), 551–559.
- Buaron, B., Reznik, D., Gilron, R., & Mukamel, R. (2020). Voluntary actions modulate perception and neural representation of action-consequences in a hand-dependent manner. *Cerebral Cortex*, *30*(12), 6097–6107.
- Cao, L., Kunde, W., & Haendel, B. (2020). Rapid and accumulated modulation of action-effects on action. *Journal of Cognitive Neuroscience*, 1–9.
- Cao, L., Steinborn, M., Kunde, W., & Haendel, B. (2020). Action force modulates action binding: Evidence for a multisensory information integration explanation. *Experimental Brain Research*, *238*(9), 2019–2029.
- Cardoso-Leite, P., Mamassian, P., Schutz-Bosbach, S., & Waszak, F. (2010). A new look at sensory attenuation. Action-effect anticipation affects sensitivity, not response bias. *Psychological Science*, *21*(12), 1740–1745.
- Cavallo, A., Koul, A., Ansuini, C., Capozzi, F., & Becchio, C. (2016). Decoding intentions from movement kinematics. *Scientific Reports*, *6*, 37036.
- Comalli, D. M., Keen, R., Abraham, E. S., Foo, V. J., Lee, M. H., & Adolph, K. E. (2016). The development of tool use: Planning for end-state comfort. *Developmental Psychology*, *52*(11), 1878–1892.
- Desantis, A., Rousset, C., & Waszak, F. (2014). The temporal dynamics of the perceptual consequences of action-effect prediction. *Cognition*, *132*(3), 243–250.
- Dewey, J. A., & Carr, T. H. (2013). Predictable and self-initiated visual motion is judged to be slower than computer generated motion. *Consciousness and Cognition*, *22*(3), 987–995.
- Dirks, D. D., & Kamm, C. (1976). Psychometric functions for loudness discomfort and most comfortable loudness levels. *Journal of Speech and Hearing Research*, *19*(4), 613–627.
- Eisenberg, M., Shmuelof, L., Vaadia, E., & Zohary, E. (2011). The representation of visual and motor aspects of reaching movements in the human motor cortex. *The Journal of Neuroscience*, *31*(34), 12377–12384.
- Endo, N., Ito, T., Mochida, T., Ijiri, T., Watanabe, K., & Nakazawa, K. (2021). Precise force controls enhance loudness discrimination of self-generated sound. *Experimental Brain Research*, *239*(4), 1141–1149.
- Gelfand, S. (2010). Behavioral tests for audiological diagnosis. In *Essentials of audiology* (3rd ed.). New York: Thieme Medical Publishers, 302–231.
- Haggard, P. (2017). Sense of agency in the human brain. *Nature Reviews. Neuroscience*, *18*(4), 196–207.
- Horvath, J., Biro, B., & Neszemlyi, B. (2018). Action-effect related motor adaptation in interactions with everyday devices. *Scientific Reports*, *8*(1), 6592.
- van Kemenade, B. M., Arikan, B. E., Kircher, T., & Straube, B. (2016). Predicting the sensory consequences of one's own action: First evidence for multisensory facilitation. *Attention, Perception, & Psychophysics*, *78*(8), 2515–2526.
- Kilteni, K., & Ehrsson, H. H. (2017). Body ownership determines the attenuation of self-generated tactile sensations. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(31), 8426–8431.
- Krasovskiy, A., Gilron, R., Yeshurun, Y., & Mukamel, R. (2014). Differentiating intended sensory outcome from underlying motor actions in the human brain. *The Journal of Neuroscience*, *34*(46), 15446–15454.
- Kunde, W., Koch, I., & Hoffmann, J. (2004). Anticipated action effects affect the selection, initiation, and execution of actions. *Q J Exp Psychol A*, *57*(1), 87–106.
- Neszemlyi, B., & Horvath, J. (2017). Consequences matter: Self-induced tones are used as feedback to optimize tone-eliciting actions. *Psychophysiology*, *54*(6), 904–915.
- Neszemlyi, B., & Horvath, J. (2018). Temporal constraints in the use of auditory action effects for motor optimization. *Journal of Experimental Psychology. Human Perception and Performance*, *44*(11), 1815–1829.
- Novembre, G., Pawar, V. M., Bufacchi, R. J., Kilintari, M., Srinivasan, M., Rothwell, J. C., ... Iannetti, G. D. (2018). Saliency detection as a reactive process: Unexpected sensory events evoke Corticomuscular coupling. *The Journal of Neuroscience*, *38*(9), 2385–2397.
- Reznik, D., Guttman, N., Buaron, B., Zion-Golumbic, E., & Mukamel, R. (2021). Action-locked neural responses in auditory cortex to self-generated sounds. *Cerebral Cortex*, *31*(12), 5560–5569.
- Reznik, D., Henkin, Y., Levy, O., & Mukamel, R. (2015). Perceived loudness of self-generated sounds is differentially modified by expected sound intensity. *PLoS One*, *10*(5), Article e0127651.
- Reznik, D., Henkin, Y., Schadel, N., & Mukamel, R. (2014). Lateralized enhancement of auditory cortex activity and increased sensitivity to self-generated sounds. *Nature Communications*, *5*, 4059.
- Reznik, D., Simon, S., & Mukamel, R. (2018). Predicted sensory consequences of voluntary actions modulate amplitude of preceding readiness potentials. *Neuropsychologia*, *119*, 302–307.
- Rosenbaum, D. A., Chapman, K. M., Weigelt, M., Weiss, D. J., & van der Wel, R. (2012). Cognition, action, and object manipulation. *Psychological Bulletin*, *138*(5), 924–946.
- Schmidt, R. A., Lee, T. D., Winstein, C., Wulf, G., & Zelaznik, H. N. (2018). *Motor control and learning: A behavioral emphasis: Human kinetics*.
- Stanislaw, H., & Todorov, N. (1999). Calculation of signal detection theory measures. *Behavior Research Methods, Instruments, & Computers*, *31*(1), 137–149.
- Ulrich, R., Rinkenauer, G., & Miller, J. (1998). Effects of stimulus duration and intensity on simple reaction time and response force. *Journal of Experimental Psychology. Human Perception and Performance*, *24*(3), 915–928.
- Weiss, C., Herwig, A., & Schutz-Bosbach, S. (2011). The self in action effects: Selective attenuation of self-generated sounds. *Cognition*, *121*(2), 207–218.
- Weiss, C., & Schutz-Bosbach, S. (2012). Vicarious action preparation does not result in sensory attenuation of auditory action effects. *Consciousness and Cognition*, *21*(4), 1654–1661.
- Wolpert, D. M., & Miall, R. C. (1996). Forward models for physiological motor control. *Neural Networks*, *9*(8), 1265–1279.