Concurrently observed actions are represented not as compound actions but as independent actions

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Abstract

Recent research suggests that we can simultaneously represent the actions of multiple agents in our motor system. However, it is unclear exactly how concurrently observed actions are represented. Here, we tested two competing hypotheses. According to the independence hypothesis, concurrently observed actions are represented as independent actions. According to the compound hypothesis, they are instead integrated, whenever possible, into compound actions. In Experiment 1 ($N = 32$), we first show that the standard imitation-inhibition task with a single hand can be extended to measure automatic imitation of compound actions. In Experiments 2-5 ($N_{\text{Total}} = 368$), we then investigated the representation of concurrently observed actions by further extending this task to include two hands. The results showed that two hands performing two different actions (e.g., one hand lifts index finger, one hand lifts middle finger) produced an effect similar to that of both hands performing just one of those actions (e.g., both hands lift index finger) but different from that of both hands performing both actions together (i.e., a compound action; lift both index and middle finger). This indicates that concurrently observed actions are coded as independent actions in the motor system.

Keywords:

Automatic imitation, multiple agents, compound actions, integration

Public Significance Statement:

This study shows that concurrently observed actions are not integrated into compound actions, suggesting that the actions of different agents are processed independently in the motor system.

In social situations, we often simulate other people's actions in our motor system (Caspers et al., 2010; Naish et al., 2014). This simulation mechanism has an important social function, because it helps us recognize (Thompson et al., 2019; Urgesi et al., 2014) and predict (Aglioti et al., 2008) observed actions, thereby facilitating coordinated behavior (Colling et al., 2013; Hadley et al., 2015; Kourtis et al., 2013). As a side effect, it also triggers imitative responses (Chartrand & van Baaren, 2009; Cracco, Bardi, et al., 2018; Heyes, 2011). A prominent task to measure these responses is the imitation-inhibition task (Brass et al., 2000; Stürmer et al., 2000). In this task, participants have to respond to a symbolic cue by performing one of two actions while they see a hand on the screen performing either the same (congruent) or a different (incongruent) action. The results typically show a congruency effect, with slower and less accurate responses on incongruent than on congruent trials. This effect has been coined automatic imitation (Cracco, Bardi, et al., 2018; Heyes, 2011) and is known to be a reliable indicator (Genschow et al., 2017) of imitative response tendencies (Cracco & Brass, 2019).

Strikingly, although we are often surrounded by multiple people, research has largely ignored the question of how action perception scales up from one to many. Breaking with this tradition, a number of recent studies showed that we spontaneously track the actions of multiple agents in our motor system (Cracco et al., 2016, 2019) and therefore that motor planning can be influenced by multiple people at once (Cracco et al., 2015; Cracco & Brass, 2018a, 2018d, 2018b). Yet, the fundamental question of exactly *how* we represent the actions of multiple agents in the motor system remains to be addressed. Zooming in on this question, two hypotheses can be distinguished: the independence hypothesis and the compound hypothesis.

The independence hypothesis argues that we represent the actions of different agents as independent actions. This hypothesis is consistent with a recent computational model of

automatic imitation (Cracco & Cooper, 2019). According to this model, automatic imitation reflects long-term associations between the visual and motor codes of an action (Cooper, Catmur, et al., 2013; Cooper, Cook, et al., 2013): action observation first leads to activation of the action's visual code and this activation then spreads to the corresponding motor code, triggering an imitative response. When we observe two different actions, the model assumes that two independent visual codes become active, thereby also activating two independent motor codes. Because an important function of the motor system is to select among multiple potential actions (Cisek & Kalaska, 2010), these two motor codes subsequently compete for selection (Cracco & Cooper, 2019) and no integration takes place, neither on the visual nor on the motor level.

In contrast, the compound hypothesis argues that instead of representing them separately, we integrate concurrently observed actions into compound actions. For example, when we see one person lifting their index finger and another person lifting their middle finger, the compound hypothesis predicts that the motor system does not represent this as two independent actions (i.e., lift index finger, lift middle finger), but rather combines both individual actions into a single compound action (i.e., lift both index and middle finger). In other words, the compound hypothesis predicts that multiple lower-order actions involving a single effector are combined into a single higher-order action involving multiple effectors. This type of integrative coding is consistent with research on ensemble coding, indicating that when we see multiple stimuli, we do not code all stimuli individually but rather compute a single ensemble representation reflecting the “average stimulus” (Alvarez, 2011; McHugh et al., 2010; Sweeny et al., 2013). For instance, Haberman and Whitney (2007) showed that people can accurately identify the mean emotion in briefly shown sets of faces without being able to identify individual faces. A similar mechanism could also relatively easily be implemented in the aforementioned computational model (Cooper, Catmur, et al., 2013;

Cracco & Cooper, 2019), by linking the perceptual code of an action not only to its corresponding motor code, but also to motor codes of which the action is a constituting part.

In the current study, we sought to distinguish between the independence and compound hypothesis. In Experiment 1, we first investigated whether the standard imitation-inhibition task with one stimulus hand can be extended to measure not just automatic imitation of single movements (lift index or middle finger) but also of compound movements (lift both index and middle finger). In Experiments 2-5, we then addressed our main question by further extending this task to two stimulus hands performing identical or different movements. In these experiments, participants watched two hands lifting either the index or middle finger (single movement stimuli), two hands lifting both the index and middle finger (compound movement stimuli), or two hands of which one hand lifted the index finger and the other hand lifted the middle finger (mixed movement stimuli). At the same time, they had to respond by lifting their own index or middle finger (single response) or by lifting both these fingers at the same time (compound response). According to the compound hypothesis, when one stimulus hand lifts the index finger and the other stimulus hand lifts the middle finger, this should trigger a compound response (i.e., lifting both fingers). As a result, mixed movement stimuli should have a similar influence as compound movement stimuli: they should facilitate the execution of compound responses. According to the independence hypothesis, however, mixed movement stimuli should instead trigger two independent responses. That is, they should simultaneously trigger an index finger response and a middle finger response (Cracco & Cooper, 2019). As a result, mixed movement stimuli should have a similar influence as single movement stimuli: they should facilitate the execution of single responses.

Open Science and Ethics Statement

Experiments 3-5 were preregistered. The experiment scripts, stimuli, data, and analysis scripts of all experiments are available on the Open Science Framework (<https://osf.io/gua5x/>). The research reported in this paper was approved by the Institutional Ethics Committee of the Faculty of Psychology and Educational Sciences at Ghent University (2018/50/Emiel Cracco).

Experiment 1

Methods

Participants. The sample size of Experiment 1 was based on an a-priori power analysis aiming for 80% power to detect a medium-sized effect of $d_z = 0.50$. This effect size was a conservative estimate obtained by roughly halving the effect size of $d_z = 0.95$ found for the standard imitation-inhibition task in a recent meta-analysis (Cracco, Bardi, et al., 2018). Based on our power analysis, 35 right-handed paid participants with normal or corrected-to-normal vision were collected on Prolific. Participants performed the experiment online in their browser window. In line with our previous work (e.g., Cracco & Brass, 2018b; De Souter et al., 2021), we excluded participants if they indicated that they had not used their right hand in the task or if their overall reaction time (RT) or error rate (ER) exceeded the sample mean by ≥ 3 SD. This resulted in the exclusion of three participants who did not use their right hand. The final sample thus consisted of 32 participants (15 female, 17 male, $M_{\text{age}} = 22.22$, $SD_{\text{age}} = 3.98$).

Task and Procedure. The experiment was an adapted version of the imitation-inhibition task (Brass et al., 2000), programmed in JsPsych (de Leeuw & Motz, 2016). Participants responded to a red, green, or blue square requesting them to lift either their right index finger, right middle finger, or both fingers (counterbalanced). Meanwhile, a virtual hand

(Haupt, 2012) was presented on the screen that either did not move or also lifted its index finger, middle finger, or both fingers. Each of these 12 trial types (4 stimuli x 3 responses) was presented equally often per block, in random order. Participants held down the G and H keys of their keyboard with their right hand throughout the experiment and responded by releasing one or both of those keys, depending on the color of the square. A response was registered as a compound response (i.e., lifting both fingers) when the two keys were released within 150 ms of each other.

Each trial started with a picture of the hand in resting position for 500 ms. The hand was presented sideways with the fingers pointing to the right, together with a black square in between the hand's index and middle finger. This picture was then replaced by a picture of the hand performing either a movement or no movement, together with a blue, red, or green square signaling the required response. The second picture was presented for 2,000 ms, or until the response, and was followed by a black screen for 1,000 ms, after which the next trial started. The experiment started with a practice phase of 30 trials with accuracy feedback, which was repeated until an accuracy level of at least 80% was reached. This was followed by 4 blocks of 60 trials without accuracy feedback. After each block, participants could take a self-paced break. After the experiment, participants were asked to report which hand they had used to respond.

Data Analysis. The task measured two forms of congruency: identity and number congruency. Identity congruency refers to whether the participant had to lift the same finger(s) as the stimulus hand; number congruency refers to whether the participant had to lift the same *number* of fingers as the stimulus hand. On most trials, identity and number congruency overlapped. However, on trials where participants had to lift one finger (e.g., index finger) and the stimulus hand lifted the opposite finger (middle finger), they were inversely related. Given that the aim of this study was not to disentangle identity and number

congruency, we discarded those trials (but see Supplementary Material for an analysis disentangling both forms of congruency and showing that they both contribute). Hence, trials that were (in)congruent in terms of number congruency were also (in)congruent in terms of identity congruency. In line with our previous work (e.g., Cracco & Brass, 2018b; De Souter et al., 2021), we also excluded trials from both the RT and ER analyses if no response was provided before the response deadline (0.35%) or if the RT was < 100 ms (0.16%) and we excluded trials from the RT but not the ER analysis if the response was incorrect (3.52%) or if the RT exceeded the participant's mean RT by ≥ 3 SD (2.10%). RTs were used as the primary dependent measure in all experiments because a recent meta-analysis showed that they are more sensitive than ERs (Cracco, Bardi, et al., 2018), but ERs were also analyzed to rule out speed-accuracy trade-offs. The data were analyzed using a stimulus movement (single, neutral, or compound) x response (single or compound) repeated measures ANOVA (Figure 1) and post-hoc tests were corrected for multiple comparisons using Holm's correction (Holm, 1979).

Figure 1*Example stimuli of Experiments 1-5*

Note. In Experiment 1, participants saw a hand lifting the index or middle finger (single movement stimulus), lifting none of its fingers (neutral stimulus), or lifting both the index and middle finger (compound movement stimulus). In Experiment 2, participants saw two hands both lifting the index or middle finger (single movement stimulus), each lifting a different finger (mixed movement stimulus), or both lifting both the index and middle finger (compound movement stimulus). Participants responded to the colored square by lifting their index or middle finger (single responses) or both fingers at the same time (compound response). Note that single response trials were excluded from the analysis when participants had to lift the opposite finger as the stimulus hand (e.g., stimulus hand lifts index finger, participant has to lift middle finger), because these were trials where identity and number

congruency were inversely related (see Methods and Supplementary Material for more details). The stimuli used in Experiment 3 were identical to those used in Experiment 2, except that only mixed and compound stimulus movements were included. The stimuli used in Experiments 4-5 were identical to those used in Experiment 2, except that different response cues were used. In those two experiments, participants had to lift their right index or right middle finger when the square was colored blue or green (counterbalanced) and both fingers at the same time when it was colored cyan (i.e., the combination of blue and green).

Results

If the imitation-inhibition task can be used to measure automatic imitation of compound movements, we should see a stimulus movement x response interaction. On single response trials, this should be reflected by slower RTs and higher ERs for compound than for single movement stimuli. In contrast, on compound response trials, it should be reflected by faster RTs and lower ERs for compound than for single movement stimuli.

The RT analysis (Figure 2) revealed a main effect of response, $F(1, 31) = 29.08, p < .001, \eta^2_p = 0.48, 95\% \text{ CI} = [.26, .62]$, with compound responses being slower than single responses, but no main effect of stimulus movement, $F(2, 30) = 0.62, p = .543, \eta^2_p = 0.04, 95\% \text{ CI} = [.00, .15]$. Crucially, the stimulus movement x response interaction was also significant, $F(2, 30) = 24.89, p < .001, \eta^2_p = 0.62, 95\% \text{ CI} = [.40, .72]$. Separate post-hoc analyses for the two responses revealed evidence for automatic imitation of compound movements. Single responses were slower for compound stimuli than for both neutral, $t(31) = 5.43, p < .001, d_z = 0.95, 95\% \text{ CI} = [0.53, 1.38]$, and single stimuli, $t(31) = 5.60, p < .001, d_z = 0.99, 95\% \text{ CI} = [0.56, 1.41]$, but did not differ between neutral and single stimuli, $t(31) = 1.13, p = .267, d_z = 0.20, 95\% \text{ CI} = [-0.15, 0.55]$. In contrast, compound responses were not slower but faster for compound stimuli than for both neutral, $t(31) = 3.86, p = .001, d_z = 0.68,$

95% CI = [0.29, 1.06], and single stimuli, $t(31) = 5.94$, $p < .001$, $d_z = 1.05$, 95% CI = [0.61, 1.48], and were faster for neutral than for single stimuli, $t(31) = 2.13$, $p = .041$, $d_z = 0.38$, 95% CI = [0.02, 0.73].

Figure 2

Results of Experiment 1

Note. Experiment 1 reaction times in ms (left) and error rates in % (right) for single and compound responses, separately for single, neutral, and compound stimulus movements. Boxplots show the mean instead of the median to match the statistical analysis. Note that trials where identity and number congruency were inversely related were not included in the analysis. This means that the single stimulus movement/single response condition included only trials where participants had to lift the same finger as the one lifted by the stimulus hand.

The ER analysis (Figure 2) revealed neither a main effect of response, $F(1, 31) = 0.01$, $p = .912$, $\eta^2_p = .00$, 95% CI = [.00, .03], nor a main effect of stimulus movement, $F(2, 30) = 1.45$, $p = .250$, $\eta^2_p = .09$, 95% CI = [.00, .23], but again showed a stimulus movement x response interaction, $F(2, 30) = 10.10$, $p < .001$, $\eta^2_p = .40$, 95% CI = [.15, .54]. Splitting up

this interaction for the two responses revealed, similar to RTs, that single responses were more error-prone for compound stimuli than for both neutral, $t(31) = 4.78, p < .001, d_z = 0.85$, 95% CI = [0.44, 1.25], and single stimuli, $t(31) = 4.56, p < .001, d_z = 0.81$, 95% CI = [0.40, 1.20], but did not differ between neutral and single stimuli, $t(31) = 0.78, p = .444, d_z = 0.14$, 95% CI = [-0.21, 0.48]. In contrast, compound responses did not differ significantly between the three types of stimuli, all $t(31) \leq 2.14, p \geq .122, d_z \leq 0.38$, although the numerical pattern was similar to RTs.

Discussion

The aim of Experiment 1 was to examine if the standard imitation-inhibition task (Brass et al., 2000) can be extended to measure automatic imitation of compound movements. To this end, we presented a hand on the screen that lifted either its index finger, its middle finger, or both fingers at the same time. Participants, in turn, responded to a colored square by also lifting their index finger, middle finger, or both fingers. In support of our hypothesis, the results revealed that participants were faster to lift a single finger when the stimulus hand also lifted only that finger and faster to lift both fingers when the stimulus hand also lifted both fingers. Interestingly, however, we found no facilitation from congruent relative to neutral stimuli on single response trials. This result is inconsistent with the standard imitation-inhibition task, where such facilitation is routinely observed (e.g., Genschow et al., 2017). Although speculative, its absence here potentially reflects a floor effect on trials where participants had to lift just one finger, as single responses were generally faster than compound responses.

Regardless of the lack of facilitation on single response trials, Experiment 1 clearly showed that seeing a compound movement primes a compound response. Therefore, Experiment 1 confirms that we can use our adapted version of the imitation-inhibition task to

investigate the main question of this study: if instead of one hand, we see two hands lifting two different fingers, how do we represent their movements? In a previous study, we found evidence that such movements are coded independently (Cracco et al., 2015; see also Cracco & Brass, 2018c). More specifically, in that study, participants responded to symbolic cues by moving one of two fingers while they saw two hands either not moving or moving two different fingers, one congruent and one incongruent. The results revealed that responses did not differ between these two conditions, even though the movements of both stimulus hands were processed. This suggests that seeing two different movements simultaneously triggered a congruent and an incongruent response that competed for execution and therefore cancelled each other out.

Importantly, however, the procedure of Cracco et al. (2015) did not allow for integrative coding because it defined an explicit response set that did not include compound responses. Hence, an important question is how the motor system processes two hands making different movements when the response set does include compound responses. According to the independence hypothesis (Figure 3), such “mixed movement” stimuli should still activate two independent responses. Given that both responses involve only one finger, this should produce similar effects as seeing a single movement: it should lead to facilitation when the required response also involves one finger (single response trials) but to interference when the required response involves two fingers (compound response trials). Note that this is true even though on single response trials, mixed movement stimuli only activate the correct response category (i.e., a single finger response) and not the correct response (i.e., an index or middle finger response). Indeed, Experiment 1 showed that activating the correct response on single response trials (by showing single movement stimuli) did not produce additional facilitation. In contrast to the independence hypothesis, the compound hypothesis (Figure 3) predicts that seeing two different movements should not activate two responses involving a

single finger but a single response involving two fingers. As a result, mixed movement stimuli should produce similar effects as compound movement stimuli: they should lead to facilitation when the required response also involves two fingers (compound response trials) but to interference when the required response involves only one finger (single response trials).

Figure 3

Predicted Results of Experiment 2 According to Both Hypotheses

Note. Expected RT pattern for Experiment 2 according to the independence and compound hypotheses. According to the independence hypothesis, mixed movement stimuli activate single finger responses. As a result, they should produce similar effects as single movement stimuli. According to the compound hypothesis, mixed movement stimuli activate compound responses. As a result, they should produce similar effects as compound movement stimuli.

Experiment 2

Methods

Participants. The sample of Experiment 2 consisted of 60 paid, right-handed participants with normal or corrected-to-normal vision, collected on Prolific. As in Experiment 1, participants performed the experiment online in their browser window. The sample size of $N = 60$ was based on the RT difference for compound responses between neutral and single movement stimuli in Experiment 1. This difference was chosen as a conservative estimate of the expected effect size for the compound hypothesis and led to a sample providing us with slightly more than 80% power to detect $d_z = 0.38$ (rounded up from $N = 57$). Participants were excluded if they indicated that they had not used their right hand in the task or if their overall RT or ER exceeded the sample mean by ≥ 3 SD. This resulted in the exclusion of two participants who had not used their right hand, two participants with an excessive ER, and one participant with an excessive RT. The final sample thus consisted of 55 participants (20 female, 35 male, $M_{\text{age}} = 25.55$, $SD_{\text{age}} = 4.94$).

Task and Procedure. Similar to Experiment 1, participants in Experiment 2 responded to one of three colored squares (red, green, or blue) by lifting their right index finger (single response), right middle finger (single response), or both fingers together (compound response). At the same time, two hands on the screen both lifted the same individual finger (single movement stimuli), the same two fingers (compound movement stimuli), or two different fingers (mixed movement stimuli). Compared to Experiment 1, the task of Experiment 2 differed only in two aspects. First, instead of one hand, participants now saw two hands (Figure 1). To ensure that all trials were comparable, both hands always made a movement. Second, because Experiment 2 included 5 instead of 4 possible stimulus movements (index/index, middle/middle, index/middle, middle/index, both/both), there were now 75 instead of 60 trials per block (i.e., 5 repetitions per unique trial type).

Data Analysis. In line with Experiment 1, we excluded trials for which identity and number congruency were inversely related. In addition, we excluded trials from both the RT and ER analysis if no response was provided (0.19%) or if the RT was < 100 ms (0.04%) and from the RT but not the ER analysis if the response was incorrect (6.03%) or if the RT exceeded the participant's mean RT by ≥ 3 SD (1.55%). The data were analyzed with a stimulus movement (single, mixed, or compound) x response (single or compound) repeated measures ANOVA and post-hoc tests were corrected for multiple comparisons using Holm's correction (Holm, 1979).

Results

Both the independence and compound hypothesis predict a stimulus movement x response interaction, but with a different pattern (Figure 3). If mixed movement stimuli are represented as two independent movements, the RT/ER pattern for single responses should be *single movement stimuli = mixed movement stimuli < compound movement stimuli* and the RT/ER pattern for compound responses should be *single movement stimuli = mixed movement stimuli > compound movement stimuli*. In contrast, if they are represented as compound movements, the RT/ER pattern for single responses should be *single movement stimuli < mixed movement stimuli = compound movement stimuli* and the RT/ER pattern for compound responses should be *single movement stimuli > mixed movement stimuli = compound movement stimuli*.

The RT analysis (Figure 4) revealed a main effect of response, $F(1, 54) = 25.08, p < .001, \eta^2_p = .32, 95\% \text{ CI} = [.15, .45]$, with compound responses being slower than single responses, but no main effect of stimulus movement, $F(2, 53) = 0.73, p = .488, \eta^2_p = 0.03, 95\% \text{ CI} = [.00, .11]$. As in Experiment 1, the stimulus movement x response interaction was also significant, $F(2, 53) = 41.28, p < .001, \eta^2_p = 0.61, 95\% \text{ CI} = [.45, .69]$. Post-hoc analyses

performed separately for the two responses showed that mixed movement stimuli had a similar influence on behavior as single movement stimuli. On single response trials, this was evidenced by faster responses for mixed stimuli than for compound stimuli, $t(54) = 6.02$, $p < .001$, $d_z = 0.81$, 95% CI = [0.50, 1.11], but not single stimuli, $t(54) = 1.29$, $p = .203$, $d_z = 0.17$, 95% CI = [-0.09, 0.44]. On compound response trials, it was evidenced by slower responses for mixed stimuli than for compound stimuli, $t(54) = 5.39$, $p < .001$, $d_z = 0.73$, 95% CI = [0.43, 1.02], but not single stimuli, $t(54) = 0.41$, $p = .687$, $d_z = 0.06$, 95% CI = [-0.21, 0.32]. Finally, in line with Experiment 1, single responses were also faster, $t(54) = 7.03$, $p < .001$, $d_z = 0.95$, 95% CI = [0.63, 1.26], and compound responses slower, $t(54) = 5.93$, $p < .001$, $d_z = 0.80$, 95% CI = [0.49, 1.10], for single movement stimuli than for compound movement stimuli.

The ER analysis (Figure 4) revealed neither a main effect of response, $F(1, 54) = 0.07$, $p = .789$, $\eta^2_p = 0.00$, 95% CI = [.00, .05], nor of stimulus movement, $F(2, 53) = 0.81$, $p = .450$, $\eta^2_p = 0.03$, 95% CI = [.00, .11], but did show a stimulus movement x response interaction, $F(2, 53) = 23.51$, $p < .001$, $\eta^2_p = 0.47$, 95% CI = [.29, .58]. Splitting up this interaction by response revealed a similar pattern as for RTs. Single responses were less error-prone for mixed than for compound stimuli, $t(54) = 5.77$, $p < .001$, $d_z = 0.78$, 95% CI = [0.47, 1.08], but did not differ between mixed and single stimuli, $t(54) = 0.02$, $p = .983$, $d_z = 0.00$, 95% CI = [-0.26, 0.27]. In contrast, compound responses were more error-prone for mixed than for compound stimuli, $t(54) = 3.85$, $p < .001$, $d_z = 0.52$, 95% CI = [0.24, 0.80], but also did not differ between mixed and single stimuli, $t(54) = 0.70$, $p = .490$, $d_z = 0.09$, 95% CI = [-0.17, 0.36]. Finally, in line with RTs, single responses were less error-prone, $t(54) = 5.93$, $p < .001$, $d_z = 0.80$, 95% CI = [0.49, 1.10], and compound responses more error-prone, $t(54) = 4.34$, $p < .001$, $d_z = 0.58$, 95% CI = [0.30, 0.87], for single compared with compound stimulus movements.

Figure 4*Results of Experiment 2*

Note. Experiment 2 reaction times in ms (left) and error rates in % (right) for single and compound responses, separately for single, mixed, and compound stimulus movements.

Boxplots show the mean instead of the median to match the statistical analysis. Note that trials where identity and number congruency were inversely related were not included in the analysis. This means that the single stimulus movement/single response condition included only trials where participants had to lift the same finger as the one lifted by the stimulus hand.

Discussion

Experiment 2 tested the main question of this study: do we represent concurrently observed actions independently in our motor system, or do we integrate them into compound actions? The results indicated that seeing two hands lift two different fingers had a similar effect as seeing two hands lift the same single finger, and this effect was clearly different from that of seeing two hands lift both the index and middle finger. These results support the independence hypothesis, meaning that the actions of the two hands were represented in the motor system not as a compound action but as two independent actions. In particular, it

suggests that two independent responses get activated when we see two hands lifting two different fingers. Because both responses involve a single finger, this causes interference when a compound response is required but facilitation when a single response is required. Importantly, facilitation from mixed stimuli on single response trials was necessarily partial facilitation because only one of the two evoked responses was the correct response. This raises the question, however, why single responses did not differ between mixed and single stimulus movements, as the latter activated not only the correct response type (single vs compound), but also the correct finger. The explanation for this is offered by the results of Experiment 1, where we likewise found no facilitation from single relative to neutral stimuli. In other words, there appears to be a floor effect on single response trials as a result of which single movement stimuli do not differ from neutral (Experiment 1) or mixed movement stimuli (Experiment 2).

Taken together, the results of Experiment 2 thus support the independence hypothesis. However, an alternative explanation could also be that responses to compound stimuli deviated from responses to the other stimuli because compound stimuli were more salient. Indeed, compound stimuli differed from the other stimuli in that they were the only stimuli where the hands lifted two fingers each. This, in turn, could have caused participants to represent those stimuli separately from the others. If true, then the fact that compound stimuli occurred only on 1/5th of the trials, likely made them pop out, potentially explaining why they influenced behavior differently than the other stimuli. To rule out this explanation, Experiment 3 included *only* mixed or compound stimuli. Furthermore, each participant saw only one type of mixed stimulus (i.e., either left hand index/right hand middle or left hand middle/right hand index). If the results of Experiment 2 can be explained by stimulus saliency, we should no longer see a difference between compound and mixed stimuli in Experiment 3. Alternatively, if they are explained by mixed movement stimuli being

represented as two independent movements, we should again see that single responses are faster but compound responses slower to mixed than to compound movement stimuli.

Experiment 3

Methods

Participants. Experiment 3 was preregistered (https://aspredicted.org/blind.php?x=RPP_BD9). The aspired sample size of Experiment 3 was based on Experiment 2. Hence, we collected data on Prolific from 60 paid, right-handed participants with normal or corrected-to-normal vision. Participants were excluded if they indicated that they had not used their right hand in the task or if their overall RT or ER exceeded the sample mean by ≥ 3 SD. This resulted in the exclusion of one participant with an excessive ER. The final sample thus consisted of 59 participants (30 female, 27 male, 2 non-binary, $M_{\text{age}} = 26.27$, $SD_{\text{age}} = 5.28$).

Task and Procedure. The task of Experiment 3 was identical to Experiment 2, with two exceptions. First, we now presented only mixed or compound stimulus movements. Second, in the mixed stimulus condition, each participant saw only one possible combination of movements: either the left hand lifting the index finger and the right hand lifting the middle finger, or the left hand lifting the middle finger and the right hand lifting the index finger. Which hand performed which movement on mixed stimulus trials was counterbalanced across participants.

Data Analysis. In line with the previous experiments, we excluded trials from both the RT and ER analysis if no response was provided (0.06%) or if the RT was < 100 ms (0.01%) and from the RT but not the ER analysis if the response was incorrect (4.79%) or if the RT exceeded the participant's mean RT by ≥ 3 SD (1.32%). The data were analyzed with a stimulus movement (mixed or compound) x response (single or compound) repeated

measures ANOVA and post-hoc tests were corrected for multiple comparisons using Holm's correction (Holm, 1979).

Results

If mixed movement stimuli are represented as two independent movements, the RT/ER pattern should be similar to Experiment 2, with *mixed movement stimuli* < *compound movement stimuli* for single responses and *mixed movement stimuli* > *compound movement stimuli* for compound responses. In contrast, if mixed movement stimuli are represented as compound movements, the RT/ER pattern should be *mixed movement stimuli* = *compound movement stimuli* for both responses.

The RT analysis (Figure 5) revealed a main effect of response, $F(1, 58) = 25.66, p < .001, \eta^2_p = .31, 95\% \text{ CI} = [.15, .44]$, with compound responses being slower than single responses, but no main effect of stimulus movement, $F(1, 58) = 1.37, p = .247, \eta^2_p = 0.02, 95\% \text{ CI} = [.00, .12]$. Importantly, in line with Experiment 2, the stimulus movement x response interaction was again significant, $F(1, 58) = 13.20, p < .001, \eta^2_p = 0.19, 95\% \text{ CI} = [.06, .32]$. Post-hoc analyses showed that single responses were faster for mixed than for compound stimuli, $t(58) = 3.64, p = .001, d_z = 0.47, 95\% \text{ CI} = [0.20, 0.74]$. No difference was observed for compound responses, $t(58) = 1.62, p = .113, d_z = 0.21, 95\% \text{ CI} = [-0.05, 0.47]$, but similar to Experiment 2, they were numerically slower for mixed than for compound stimuli.

The ER analysis (Figure 5) revealed no main effect of response, $F(1, 58) = 1.43, p = .236, \eta^2_p = 0.02, 95\% \text{ CI} = [.00, .12]$, nor of stimulus movement, $F(1, 58) = 0.16, p = .691, \eta^2_p = 0.00, 95\% \text{ CI} = [.00, .06]$, but again showed a stimulus movement x response interaction, $F(1, 58) = 17.89, p < .001, \eta^2_p = 0.24, 95\% \text{ CI} = [.09, .37]$. Post-hoc analyses showed that single responses were less error-prone for mixed than for compound stimuli, $t(58) = 4.06, p <$

.001, $d_z = 0.53$, 95% CI = [0.25, 0.80], whereas compound responses were more error-prone for mixed than for compound stimuli, $t(58) = 2.76$, $p = .008$, $d_z = 0.36$, 95% CI = [0.09, 0.62].

Figure 5

Results of Experiment 3

Note. Experiment 3 reaction times in ms (left) and error rates in % (right) for single and compound responses, separately for mixed and compound stimulus movements. Boxplots show the mean instead of the median to match the statistical analysis.

Discussion

Experiment 3 tested whether mixed and compound stimulus movements still exerted a different influence on behavior when compound stimuli no longer stood out. Although the difference became smaller when both types of stimuli were matched in terms of frequency, it was still there. This indicates that increased attentional capture of compound stimuli might have explained part of the difference observed in Experiment 2, but not the entire difference. Instead, Experiment 3 indicates that the difference between mixed and compound movement

stimuli is better explained by the hypothesis that concurrently observed actions are processed in the motor system as two independent actions rather than as one integrated action.

An important question that remains, however, is whether action coding depends on task context. That is, certain aspects of the task used in Experiments 2-3 may have disrupted integrative coding. First, the two stimulus hands used in the task were two identical (mirrored) hands. As a result, it is possible that participants represented their movements not as the movements of two persons but as bimanual movements. This, in turn, could have disrupted integration of the two individual actions into a compound action that can be executed with a single hand. Second, the imperative cue appeared together with the stimulus movement. Integrative coding is likely to take time, however. Indeed, previous research suggests that top-down effects on imitative behavior may become apparent only when the cue is presented after the stimulus movement (Cracco, Genschow, et al., 2018). Finally, Experiments 2-3 used three independent cues (i.e., red, green, and red) for the three possible responses. This, in turn, could have probed participants to represent the compound response as independent from the other two responses. To address these issues, Experiment 4 used the same task as Experiment 2, but with two different stimulus hands, with a delay between the presentation of the stimulus movements and response cue, and with a cue for compound responses that was no longer an independent cue, but rather a mix of the cues used for index and middle finger responses.

Experiment 4

Methods

Participants. Experiment 4 was preregistered (https://aspredicted.org/YK6_MSU). The aspired sample size of Experiment 4 was $N = 120$. This was based on an a-priori power analysis assuming 90% power for a small effect size of $d_z = 0.30$. Experiment 4 assumed a smaller effect size than Experiment 2 to account for the possibility that the difference between

mixed and single movement stimuli, which would point towards integrative coding¹, may have been too small to detect in Experiment 2. To compensate for drop-out, as preregistered, data from 130 paid, right-handed participants with normal or corrected-to-normal vision was collected on Prolific. Participants were excluded if they indicated that they had not used their right hand in the task or if their overall RT or ER exceeded the sample mean by ≥ 3 SD. This resulted in the exclusion of one participant who had not used their right hand, three participants with an excessive ER, and one participant with an excessive RT. Thus, the final sample consisted of 126 participants (69 female, 56 male, 1 non-binary, $M_{\text{age}} = 25.39$, $SD_{\text{age}} = 4.33$).

Task and Procedure. The task of Experiment 4 was the same as Experiment 2, with the following differences. First, the two stimulus hands now had a different skin tone. That is, one hand had a pale skin tone and one hand had a dark skin tone (counterbalanced; Figure 1). Importantly, previous research has shown that skin tone as such does not influence automatic imitation, not even when tested in large samples ($N = 297$ and $N = 737$; Genschow et al., 2021). After the experiment, participants were asked whether they thought the hands belonged to two different persons or to the same person. This revealed that 78% of the participants perceived the hands as belonging to two different persons. Participants who did not perceive the hands as different persons were retained in the sample, but excluding them did not change the results.

Second, the cue was now presented 100 ms after the stimulus movement, consistent with previous research showing that top-down effects on imitation can be captured with such a delay (Cracco, Genschow, et al., 2018). Finally, the cues for index and middle finger responses were now either blue or green (counterbalanced) and the cue for compound

¹ It is possible that the two stimulus movements in the mixed stimulus condition are only partially integrated, in which case these stimuli would produce different effects than both single and compound stimulus movements.

responses was always cyan (i.e., the combination of blue and green). During the instructions, this was explained to participants to make it more likely that they would encode compound responses not as a separate response but as the combination of the index and middle finger response.

Data Analysis. In line with Experiments 1-2, we excluded trials for which identity and number congruency were inversely related. In addition, we also excluded trials from both the RT and ER analysis if no response was provided (0.16%) or if the RT was < 100 ms (0.05%) and from the RT but not the ER analysis if the response was incorrect (5.66%) or if the RT exceeded the participant's mean RT by ≥ 3 SD (1.41%). The data were analyzed with a stimulus movement (single, mixed, or compound) x response (single or compound) repeated measures ANOVA and post-hoc tests were corrected using Holm's correction (Holm, 1979).

Results

The expected results were identical to Experiment 2 (Figure 3). The RT analysis (Figure 6) revealed a main effect of response, $F(1, 125) = 83.75, p < .001, \eta^2_p = .40, 95\% \text{ CI} = [.29, .48]$, with compound responses being slower than single responses, but no main effect of stimulus movement, $F(2, 124) = 0.58, p = .561, \eta^2_p = 0.01, 95\% \text{ CI} = [.00, .04]$. As in Experiment 2, the stimulus movement x response interaction was also significant, $F(2, 124) = 98.08, p < .001, \eta^2_p = 0.61, 95\% \text{ CI} = [.52, .67]$. Post-hoc analyses performed separately for the two responses revealed a similar pattern as in Experiment 2, with mixed movement stimuli having a similar influence as single movement stimuli. On single response trials, this was evidenced by faster responses for mixed stimuli than for compound stimuli, $t(125) = 11.02, p < .001, d_z = 0.98, 95\% \text{ CI} = [0.77, 1.19]$, but not single stimuli, $t(125) = 0.16, p = .874, d_z = 0.01, 95\% \text{ CI} = [-0.16, 0.19]$. On compound response trials, it was evidenced by slower responses for mixed stimuli than for compound stimuli, $t(125) = 10.88, p < .001, d_z =$

0.97, 95% CI = [0.76, 1.18], but not single stimuli, $t(125) = 0.06$, $p = .950$, $d_z = 0.00$, 95% CI = [-0.17, 0.18]. Finally, replicating Experiment 1, single responses were also faster, $t(125) = 10.32$, $p < .001$, $d_z = 0.92$, 95% CI = [0.71, 1.13], and compound responses slower, $t(125) = 10.54$, $p < .001$, $d_z = 0.94$, 95% CI = [0.73, 1.15], for single than for compound stimuli.

Figure 6

Results of Experiment 4

Note. Experiment 4 reaction times in ms (left) and error rates in % (right) for single and compound responses, separately for single, mixed, and compound stimulus movements. Boxplots show the mean instead of the median to match the statistical analysis. Note that trials where identity and number congruency were inversely related were not included in the analysis. This means that the single stimulus movement/single response condition included only trials where participants had to lift the same finger as the one lifted by the stimulus hand.

The ER analysis (Figure 6) revealed neither a main effect of response, $F(1, 125) = 2.99$, $p = .086$, $\eta^2_p = 0.02$, 95% CI = [.00, .08], nor a main effect of stimulus movement, $F(2, 124) = 0.246$, $p = .782$, $\eta^2_p = 0.00$, 95% CI = [.00, .03], but again a significant stimulus

movement x response interaction, $F(2, 124) = 36.90, p < .001, \eta^2_p = 0.37, 95\% \text{ CI} = [.26, .46]$. Splitting up this interaction by response revealed a similar pattern as for RTs. That is, single responses were less error-prone for mixed than for compound stimuli, $t(125) = 6.52, p < .001, d_z = 0.58, 95\% \text{ CI} = [0.39, 0.77]$, but did not differ between mixed and single stimuli, $t(125) = 0.38, p = .700, d_z = 0.03, 95\% \text{ CI} = [-0.14, 0.21]$. In contrast, compound responses were more error-prone for mixed than for compound stimuli, $t(125) = 5.40, p < .001, d_z = 0.48, 95\% \text{ CI} = [0.30, 0.67]$, but also did not differ between mixed and single stimuli, $t(125) = 0.52, p = .607, d_z = 0.05, 95\% \text{ CI} = [-0.13, 0.22]$. Finally, single responses were again less error-prone, $t(125) = 7.08, p < .001, d_z = 0.63, 95\% \text{ CI} = [0.44, 0.82]$, and compound responses more error-prone, $t(125) = 6.16, p < .001, d_z = 0.55, 95\% \text{ CI} = [0.36, 0.74]$, for single stimuli than for compound stimuli.

Discussion

Experiment 4 tested whether evidence for integrative action coding would appear if there was more time to process the movements and if aspects of the task were changed to facilitate integration. That is, in contrast to Experiment 2, Experiment 4 showed two different hands and encouraged participants to code the compound response as a combination of the index and middle finger response by using a cue for compound responses that mixed together the cues used for index and middle finger responses. Yet, despite these changes, the results of Experiment 4 were remarkably similar to those of Experiment 2. That is, the results revealed that mixed movement stimuli had a similar influence on behavior as single movement stimuli, but a different influence than compound movement stimuli. Confirming the findings of Experiments 2-3, the results of Experiment 4 thus indicate that mixed movement stimuli were not integrated into a single compound response but were coded independently in the motor system.

The aim of Experiment 5 was to go yet one step further by introducing a collaborative context in which the two stimulus hands were seen as working together. More specifically, each block of the imitation task in Experiment 5 was preceded by a block of an inducer task. In this inducer task, the hands used in the imitation task took on the role of “followers” in a setup where they had to copy the actions of an “instructor” hand lifting either the index finger, the middle finger, or both fingers (Figure 7). Importantly, when the instructor hand lifted both fingers, the follower hands had to work together to do the task. In that case, one hand had to lift the index finger and one hand had to lift the middle finger. After each trial, participants had to indicate whether the follower hands had correctly copied the instructor hand. This procedure achieved two things. First, it created a collaborative context in which participants observed the hands working together. Second, it established an association between mixed and compound movements. If integrative coding occurs when promoted by the context, mixed movement stimuli should now have an influence that is more similar to compound movement stimuli. If, instead, mixed movement stimuli are still processed as independent movements despite the context, they should again have a similar influence as single movement stimuli.

Experiment 5

Methods

Participants. Experiment 5 was preregistered (https://aspredicted.org/MLJ_J1Z). Similar to Experiment 4, the aspired sample size of Experiment 5 was $N = 120$, but we collected data from 130 paid, right-handed participants with normal or corrected-to-normal vision on Prolific to compensate for potential drop-out. As preregistered, because more than 10 participants had to be excluded (see below), this was increased to $N = 140$ after collecting the first 130 participants, but before data analysis. Participants were excluded if they indicated that they had not used their right hand in the task, if their ER on the inducer task was $> 20\%$,

or if their RT or ER on the imitation task exceeded the sample mean by ≥ 3 SD. This resulted in the exclusion of three participants who had not used their right hand, nine participants with an excessive inducer task ER, and one participant with an excessive imitation task ER. Thus, the final sample consisted of 128 participants (60 female, 64 male, 4 non-binary, $M_{\text{age}} = 23.39$, $SD_{\text{age}} = 3.95$).

Task and Procedure. The task of Experiment 5 was the same as the task of Experiment 4, except for three changes. First, instead of 4 blocks of 75 trials, the imitation task of Experiment 5 included only 3 blocks. Second, each block of the imitation task was now preceded by a block of the inducer task, each with 30 trials. Third, to accommodate for the addition of a second task, the practice phase now consisted of two parts. In the first part, participants practiced 10 trials of the inducer task. In the second part, participants practiced 20 trials of the imitation task. For both tasks, participants received accuracy feedback after each trial in the practice phase, but not in the experiment proper. If performance on the practiced task was below 80%, the corresponding task was repeated until performance increased above this level.

In the inducer task, three hands were presented: one instructor hand, at the top of the screen, and two follower hands, at the bottom of the screen (Figure 7). On each trial, the instructor hand made a movement that the follower hands had to copy. Participants' task was to monitor the accuracy of the followers' responses and to indicate after each trial whether the follower hands had responded correctly. The instructor could make three possible movements: lift index finger, lift middle finger, or lift both fingers. In the first two cases, the followers had to respond by both lifting the corresponding finger. In the last case, however, the followers had to work together. More specifically, when the instructor hand lifted both the index and the middle finger, one follower had to lift the index finger while the other follower had to lift the middle finger.

The follower hands responded correctly on 50% of the practice trials and on 80% of the experimental trials. Each of the 12 correct instructor-follower combinations occurred twice per block. In addition, the followers made two wrong responses to each of the 3 possible instructions per block. On these trials, they randomly performed one of the possible wrong responses. Trials were presented in random order and started with the three hands in still position for 500 ms, followed by the instructor hand making a movement. After 600 ms, the follower hands responded to the instruction and this remained on the screen for 1500 ms, followed by a screen asking participants to indicate whether the followers had responded correctly. Participants could respond by clicking one of two buttons on the screen using their computer mouse or mousepad.

Only the follower hands were used in the imitation task (Figure 1). As in Experiment 4, one hand had a dark skin tone and one hand had a pale skin tone (counterbalanced). The instructor hand's skin tone was in between that of the two follower hands, similar to Experiments 1-3. After the experiment, participants were asked whether they thought the two follower hands belonged to two different persons or to the same person. This revealed that 86% of the participants perceived the hands as belonging to two different persons. Similar to Experiment 4, excluding participants who did not consider two follower hands to be different persons did not change the results.

Data Analysis. We again excluded trials for which identity and number congruency were inversely related. In addition, we excluded trials from both the RT and ER analysis if no response was provided (0.17%) or if the RT was < 100 ms (0.02%) and from the RT but not the ER analysis if the response was incorrect (4.23%) or if the RT exceeded the participant's mean RT by ≥ 3 SD (1.59%). The data were analyzed with a stimulus movement (single, mixed, or compound) x response (single or compound) repeated measures ANOVA and post-hoc tests were corrected for multiple comparisons using Holm's correction (Holm, 1979).

Figure 7

Example stimuli of the inducer task used in Experiment 5

Note. In the inducer task of Experiment 5, participants saw one “instructor” hand (top) and two “follower” hands (bottom). First, the instructor lifted the index finger, middle finger, or both fingers. The followers then had to copy those movements. When the instructor hand lifted only one finger, the follower hands had to lift the corresponding finger. For example, if the instructor lifted the index finger, both follower hands had to lift the index finger as well. When the instructor hand lifted both fingers, the follower hands had to work together to copy the instructed movement. In that case, one hand had to lift the index finger and the other hand had to lift the middle finger. Participants had to indicate after each trial whether the follower hands had followed the instruction correctly. The two follower hands were also used in the imitation task.

Results

The expected results were identical to Experiment 2 (Figure 3). Performance on the inducer task was high, with an average accuracy of 98.66% (SD = 2.38%). The RT analysis (Figure 8) revealed a main effect of response, $F(1, 127) = 48.87, p < .001, \eta^2_p = .28$, 95% CI = [.17, .37], with compound responses being slower than single responses, but no main effect of stimulus movement, $F(2, 126) = 1.46, p = .236, \eta^2_p = 0.02$, 95% CI = [.00, .07]. As in Experiments 2-4, the stimulus movement x response interaction was also significant, $F(2, 126) = 87.86, p < .001, \eta^2_p = 0.58$, 95% CI = [.49, .65]. Post-hoc analyses for the two

responses revealed a similar pattern as in Experiments 2 and 4, with mixed movement stimuli having a similar effect as single movement stimuli. On single response trials, reaction times were faster for mixed than for compound stimuli, $t(127) = 9.79, p < .001, d_z = 0.87, 95\% \text{ CI} = [0.66, 1.07]$, but did not differ between mixed and single stimuli, $t(127) = 0.76, p = .450, d_z = 0.07, 95\% \text{ CI} = [-0.11, 0.24]$. On compound response trials, reaction times were instead slower for mixed than for compound stimuli, $t(127) = 9.11, p < .001, d_z = 0.81, 95\% \text{ CI} = [0.60, 1.01]$, but again did not differ between mixed and single stimuli, $t(127) = 0.70, p = .483, d_z = 0.06, 95\% \text{ CI} = [-0.11, 0.24]$. In line with Experiment 1, single responses were also faster, $t(127) = 7.91, p < .001, d_z = 0.70, 95\% \text{ CI} = [0.50, 0.89]$, and compound responses slower, $t(127) = 9.79, p < .001, d_z = 0.87, 95\% \text{ CI} = [0.66, 1.07]$, for single than for compound stimuli.

The ER analysis (Figure 8) revealed no main effect of response, $F(1, 127) = 1.52, p = .220, \eta^2_p = 0.01, 95\% \text{ CI} = [.00, .06]$, but did reveal a main effect of stimulus movement, $F(2, 126) = 3.522, p = .032, \eta^2_p = 0.05, 95\% \text{ CI} = [.00, .12]$, with fewer errors in the single stimulus movement condition than in the other two conditions. More importantly, there was also a stimulus movement x response interaction, $F(2, 126) = 24.90, p < .001, \eta^2_p = 0.28, 95\% \text{ CI} = [.17, .37]$. Splitting up this interaction by response revealed that single responses were less error-prone for mixed than for compound stimuli, $t(127) = 5.38, p < .001, d_z = 0.48, 95\% \text{ CI} = [0.29, 0.66]$, and slightly less error-prone for single than for mixed stimuli, $t(127) = 2.28, p = .024, d_z = 0.20, 95\% \text{ CI} = [0.03, 0.38]$. In contrast, compound responses were more error-prone for mixed than for compound stimuli, $t(127) = 4.28, p < .001, d_z = 0.38, 95\% \text{ CI} = [0.20, 0.56]$, but did not differ between mixed and single stimuli, $t(127) = 1.09, p = .279, d_z = 0.10, 95\% \text{ CI} = [-0.08, 0.27]$. Finally, single responses were again less error-prone, $t(127) = 6.39, p < .001, d_z = 0.56, 95\% \text{ CI} = [0.38, 0.75]$, and compound responses more error-prone,

$t(127) = 3.65, p < .001, d_z = 0.32, 95\% \text{ CI} = [0.14, 0.50]$, for single stimuli than for compound stimuli.

Figure 8

Results of Experiment 5

Note. Experiment 5 reaction times in ms (left) and error rates in % (right) for single and compound responses, separately for single, mixed, and compound stimulus movements. Boxplots show the mean instead of the median to match the statistical analysis. Note that trials where identity and number congruency were inversely related were not included in the analysis. This means that the single stimulus movement/single response condition included only trials where participants had to lift the same finger as the one lifted by the stimulus hand.

Discussion

Experiment 5 further primed action integration by preceding each block of the imitation task by an inducer task in which a collaborative context was established where mixed movement stimuli were actively linked to compound movement stimuli. However, despite this context, the results again revealed that mixed movement stimuli had a similar

influence on behavior as single movement stimuli, suggesting that they were processed in the motor system as independent instead of integrated movements.

It should be noted, however, that in contrast to Experiments 2 and 4, error rates on single response trials were slightly higher for mixed than for single movement stimuli. Although error rates were still lower than for compound movement stimuli, this could indicate that mixed movement stimuli were partially integrated, causing them to have a different influence than both single and compound movement stimuli. This seems unlikely, however, considering that there was no evidence for a corresponding effect on compound response trials, nor on reaction times. Indeed, even for the error rates, the evidence was weak and only barely reached the threshold for statistical significance. Together with the fact that error rates were generally low and therefore less reliable, this suggests that the difference in accuracy between single and mixed stimuli for single responses likely reflected random noise.

General Discussion

Previous research has shown that multiple observed actions can be represented simultaneously in the motor system (Cracco et al., 2015, 2016; Cracco & Brass, 2018a, 2018d, 2018b; Cracco & Cooper, 2019). However, the fundamental question of *how* they are represented remains to be addressed. In the current study, we tested two hypotheses. According to the independence hypothesis, concurrently observed actions are represented as multiple independent actions. According to the compound hypothesis, they are instead integrated, whenever possible, into a compound action. In Experiment 1, we first tested if the standard imitation-inhibition task with a single stimulus hand (Brass et al., 2000; Cracco, Bardi, et al., 2018) can be used to measure automatic imitation of compound actions. In Experiments 2-5, we then tested our two hypotheses by extending this task from one hand to two hands. The results consistently revealed that two stimulus hands lifting two different

fingers produced an effect similar to that of two hands each lifting the same single finger but different from that of both hands lifting both fingers (i.e., a compound action). This was true even when differences in stimulus frequency were controlled (Experiment 3) or when action integration was promoted by the task context (Experiments 4-5). As such, our results show that concurrently observed actions are coded separately in the motor system.

This result is consistent with a recent computational model of automatic imitation (Cooper, Catmur, et al., 2013; Cooper, Cook, et al., 2013; Cracco & Cooper, 2019). In line with the independence hypothesis, this model assumes that concurrently observed actions activate independent motor representations (Cracco & Cooper, 2019). Simulations using this model showed that it can explain a broad range of data on automatic imitation in multi-agent settings (Cracco et al., 2015; Cracco & Brass, 2018a, 2018d, 2018b) and the current results add onto this literature by providing empirical support for the model's assumption that there is no integration of observed actions in the motor system. More broadly, our findings suggest that at the motor level, compound actions are represented not as the sum of their parts but as separate actions.

An important question, however, is the extent to which this finding is specific to action observation. Given that connections between the perceptual code of an action and its motor code are thought to develop through domain-general mechanisms such as associative learning (Brass & Heyes, 2005; Cracco, Bardi, et al., 2018; Heyes, 2011), it seems likely that actions triggered by non-social events (e.g., lateralized light flashes, such as in a Simon task) would not be integrated in the motor system either, but this will have to be confirmed empirically.

If confirmed, this lack of integration may seem at odds with previous work showing that people tend to process complex visual scenes by averaging together different stimuli into ensemble representations (Alvarez, 2011; McHugh et al., 2010; Sweeny et al., 2013). Such

ensemble processing has not only been observed for static social stimuli such as faces (Haberman & Whitney, 2007, 2009) or body postures (McHugh et al., 2010), but also for moving stimuli such as biological movements (Sweeny et al., 2013). More specifically, Sweeny and colleagues (2013) showed participants brief videos of groups of point-light walkers (Johansson, 1973) who moved in different directions and asked participants to indicate the average walking direction of the crowd. The results revealed that participants were highly accurate in indicating the average group direction, even more so than in estimating the direction of the individual walkers. A crucial difference between their study and the current study, however, is that Sweeny et al. (2013) showed multiple agents all performing the same action (i.e., walking), whereas we showed multiple hands performing different actions. Hence, it is possible that ensemble processes are applied only to action parameters (e.g., movement direction, speed, force, etc.) but not to the actions themselves. Although more research is needed, this would be consistent with hierarchical models of action representation, arguing that different aspects of an action, such as action goals and action kinematics, are coded at different levels of processing (Genschow et al., 2019; Wohlschläger et al., 2003).

Another possibility is that the integration of observed actions depends on social context. For example, previous research has shown that people are faster to imitate group actions than individual actions when they themselves are part of a group, but vice versa when they are not (Tsai et al., 2011). These results suggest that social context can have a pervasive influence on how we process and respond to other people's actions in group settings. As such, an interesting hypothesis is that the integration of other people's actions into higher-order compound actions depends on whether they perform independent or joint actions. Although the results of Experiment 5 indicate that concurrently observed actions are coded as independent actions even in collaborative contexts, it cannot be ruled out that integration does

take place in more interactive situations or with more meaningful actions. Addressing this question will be an important task for future research, but goes beyond the scope of the current work, both methodologically and theoretically. Methodologically, testing this hypothesis would require fundamentally different paradigms and measures. Theoretically, the aim of this study was not to test how social context moderates action representation, but rather to test the more fundamental question of how the motor system represents concurrently observed actions. Our results show that it treats them as independent actions by default. While this does not rule out that integration might take place under specific circumstances, it does indicate that integration is not the norm, but likely requires additional processes that act upon the individual action representations by binding them together in groups (e.g., Cracco, Lee, et al., 2021).

Finally, the current study has implications for recent evidence that not just planning but also seeing two different actions elicits response conflict (Cracco, Braem, et al., 2021; Cracco et al., 2019). Because response conflict is typically elicited when two conflicting motor commands are activated, we have previously shown actions that cannot be executed together. As a result, it was unclear whether observed actions that are different but can be executed together would also elicit response conflict. Consistent with research on action planning (Botvinick et al., 2001), the current study suggests that they would. That is, our results show that different observed actions activate different motor commands even when they are not mutually exclusive in terms of motor execution. Although direct evidence is still lacking, this suggests that not only mutually exclusive but also mutually compatible observed actions generate motor conflict.

Our study also has a number of limitations. A first limitation is that an alternative explanation for Experiments 2-5 could be that participants randomly represented either the left or right hand on each trial. However, we have previously ruled out random representation

as a mechanism for automatic imitation of multiple agents in a task with very similar stimuli (Cracco & Brass, 2018a). In particular, using the same stimulus setup as in Experiments 2-5, we showed that focusing on or imitating the actions of one hand did not eliminate automatic imitation of a second, unattended hand. Similarly, using a different setup with four hands, we found evidence for automatic imitation of multiple hands even when showing *only* those hands that would make a movement on that trial (Cracco & Brass, 2018d). Together, these findings clearly show that observers do simultaneously represent the actions of multiple hands moving together.

A second limitation is that Experiments 2-5 used one left and one right stimulus hand. As a result, it is possible that participants represented the stimuli as bimanual stimuli and therefore mapped the movements of the left stimulus hand onto their left hand and the movements of the right stimulus hand onto their right hand. Since this would imply that participants always mapped only one stimulus movement onto their (right) response hand, it could provide a second alternative explanation for why seeing two different actions did not trigger a compound response. Although the fact that Experiments 3-5 used hands with different skin tones makes this less likely, it remains a theoretical possibility. Importantly, however, performance on mixed stimulus trials should then critically depend on whether the right stimulus hand performed an action that was congruent or incongruent with the response hand. As shown in Supplementary Material, this was not the case. As such, our data suggest that both stimulus movements were mapped onto the response hand. This is consistent with research showing that the effects of seeing multiple hands on automatic imitation does not depend on whether multiple identical (Cracco & Brass, 2018d, 2018b) or multiple different (Cracco et al., 2015) hands are shown, not even when the two hands are positioned in a way that resembles bimanual movements (Cracco & Brass, 2018a).

In conclusion, the current study shows that we represent concurrently observed actions as independent actions in the motor system, and not as a compound action. These results provide important insight into how models of action perception can be extended beyond the dyad.

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Supplementary Material

Disentangling Identity and Number Congruency

Results. To disentangle the effects of identity and number congruency, we restricted the analysis to single response trials (Figure S1). Specifically, we compared trials where both identity and number congruency were congruent (ID_C/NR_C) with trials where identity congruency was incongruent, but number congruency was congruent (ID_{IC}/NR_C) and trials where both identity and number congruency were incongruent (ID_{IC}/NR_{IC}). An effect of identity congruency should result in faster and more accurate responses on ID_C/NR_C trials than on ID_{IC}/NR_C trials. An effect of number congruency should result in faster and more accurate responses on ID_{IC}/NR_C trials than on ID_{IC}/NR_{IC} trials. For conciseness, the effects of identity and number congruency were tested across all experiments where they could both be isolated (Experiments 1, 2, 4, and 5) using a condition x experiment mixed measures ANOVA. Post-hoc tests were corrected for multiple comparisons using Holm's correction (Holm, 1979).

Figure S1

Design of the identity vs. number congruency analysis

Note. Example stimuli of the identity (ID) vs. number (NR) congruency analysis (columns), separately for the two responses included in the analysis (rows). Identity congruency refers to

whether the participant and stimulus hand lift the same finger(s). Number congruency refers to whether the participant and stimulus hand lift the same number of fingers. Note that the shown example stimuli are from Experiment 2. In Experiment 1, only one hand was shown. In Experiments 4-5, the two hands had a different skin tone, one dark and one light.

The RT analysis (Figure S2) revealed a main effect of condition, $F(2, 336) = 107.91, p < .001, \eta^2_p = .39, 95\% \text{ CI} = [.32, .45]$, but no main effect of experiment, $F(3, 337) = 0.37, p = .778, \eta^2_p = .00, 95\% \text{ CI} = [.00, .01]$, nor an experiment x condition interaction, $F(6, 672) = 1.10, p = .363, \eta^2_p = .01, 95\% \text{ CI} = [.00, .02]$. Follow-up tests of the condition main effect revealed both an identity congruency effect (ID_C/NR_C vs. $\text{ID}_{IC}/\text{NR}_C$), $t(340) = 3.69, p < .001, d_z = 0.20, 95\% \text{ CI} = [0.09, 0.31]$, and a number congruency effect ($\text{ID}_{IC}/\text{NR}_C$ vs. $\text{ID}_{IC}/\text{NR}_{IC}$), $t(340) = 12.12, p < .001, d_z = 0.66, 95\% \text{ CI} = [0.54, 0.77]$. The ER analysis (Figure S2) likewise revealed a main effect of condition, $F(2, 336) = 62.82, p < .001, \eta^2_p = .27, 95\% \text{ CI} = [.21, .33]$. Although it also revealed a main effect of experiment, $F(3, 337) = 4.42, p = .005, \eta^2_p = .04, 95\% \text{ CI} = [.01, .07]$, the experiment x condition interaction was not significant, $F(6, 672) = 1.17, p = .323, \eta^2_p = .01, 95\% \text{ CI} = [.00, .02]$. Follow-up tests of the condition main effect revealed a borderline non-significant identity congruency effect (ID_C/NR_C vs. $\text{ID}_{IC}/\text{NR}_C$), $t(340) = 1.81, p = .072, d_z = 0.10, 95\% \text{ CI} = [-0.01, 0.20]$, and a significant number congruency effect ($\text{ID}_{IC}/\text{NR}_C$ vs. $\text{ID}_{IC}/\text{NR}_{IC}$), $t(340) = 9.77, p < .001, d_z = 0.53, 95\% \text{ CI} = [0.42, 0.64]$.

Discussion. The results revealed an influence of both identity and number congruency. However, the effect of number congruency was substantially stronger than the effect of identity congruency. Indeed, the effect of identity congruency ($d_z = 0.20$ for RTs) was notably smaller than what is typically observed in the standard version of the imitation-inhibition task ($d_z = 1.03$; Cracco et al., 2018). A likely explanation for why this was the case

is that the number of lifted fingers was more salient than the identity of the lifted fingers and that the effect of number congruency therefore trumped the effect of identity congruency.

Figure S2

Results of the identity vs. number congruency analysis across Experiments 1, 2, 4, and 5

Note. Reaction times in ms (left) and error rates in % (right) on ID_C/NR_C, ID_{IC}/NR_C, and ID_{IC}/NR_{IC} trials. Boxplots show the mean instead of the median to match the statistical analysis.

Disentangling Unimanual and Bimanual Representation

Results. To rule out that participants represented the stimulus movements as bimanual movements and therefore mapped only the movements of the right stimulus hand on their (right) response hand, we compared single responses to index/middle and middle/index stimuli across Experiments 2, 4, and 5 using a stimulus movement (index/middle or middle/index) x response (index or middle) x experiment mixed measures ANOVA. If participants only imitated the right stimulus hand, they should have been faster to lift their right index finger on middle/index than on index/middle trials but faster to lift their right

middle finger on index/middle than on middle/index trials. In contrast, the RT analysis (Figure S5) revealed only a main effect of stimulus movement, $F(1, 306) = 8.52, p = .004, \eta^2_p = .03$, 95% CI = [.01, .06], with slower responses for middle/index than for index/middle stimuli, but no other effects, all $ps \geq .073$. Similarly, the ER analysis revealed only a main effect of response, $F(1, 306) = 8.42, p = .004, \eta^2_p = .03$, 95% CI = [.01, .06], with more errors when making middle finger responses compared with index finger responses, but no other effects, all $ps \geq .097$.

Figure S3

Results of the unimanual vs. bimanual representation analysis in Experiments 2, 4, and 5

Note. Reaction times in ms (left) and error rates in % (right) on index/middle and middle/index mixed trials, separately for index and middle finger responses. Index/middle trials are trials where the left hand lifted the index finger and the right hand lifted the middle finger. Middle/index trials are trials where the left hand lifted the middle finger and the right hand lifted the index finger. Boxplots show the mean instead of the median to match the statistical analysis.

Discussion. If participants mapped the left stimulus hand onto their left hand and the right stimulus hand onto their right (response) hand, then participants should have been faster to lift the finger that was being lifted by the right stimulus hand. In contrast, participants were generally slower when the left stimulus hand lifted the middle finger and the right stimulus hand lifted the index finger, regardless of the movement they had to perform themselves. While speculative, this could potentially be explained by spatial matching. That is, research using vertical stimulus presentations has shown that stimuli presented at the bottom trigger a left response, whereas stimuli presented at the top trigger a right response (Weeks & Proctor, 1990). Relative to each other, index finger stimuli occurred at the bottom and middle finger stimuli occurred at the top. Hence, performance may have been facilitated when the left stimulus hand was associated with a left response (i.e., index finger lift) and the right stimulus hand with a right response (i.e., middle finger lift), as was the case for index/middle stimulus movements, than when it was the other way around, as was the case for middle/index stimulus movements. This interpretation is consistent with previous evidence that orthogonal spatial compatibility influences automatic imitation when the stimulus hands are presented sideways like in the current study (Cracco et al., 2018; Shaw et al., 2017). While this interpretation will need further testing, it is clear that an explanation in terms of bimanual representation cannot explain the data.