Influence of finger and mouth action observation on random number generation: an instance of embodied cognition for abstract concepts

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ABSTRACT

Numerical magnitude and specific grasping action processing have been shown to interfere with each other because some aspects of numerical meaning may be grounded in sensorimotor transformation mechanisms linked to finger grip control. However, how specific these interactions are to grasping actions is still unknown. The present study tested the specificity of the number–grip relationship by investigating how the observation of different closing-opening stimuli that might or not refer to prehension–releasing actions was able to influence a random number generation task. Participants had to randomly produce numbers after they observed action stimuli representing either closure or aperture of the fingers, the hand or the mouth, or a colour change used as a control condition. Random number generation was influenced by the prior presentation of finger grip actions, whereby observing a closing finger grip led participants to produce small rather than large numbers, whereas observing an opening finger grip led them to produce large rather than small numbers. Hand actions had reduced or no influence on number production; mouth action influence was restricted to opening, with an overproduction of large numbers. Finally, colour changes did not influence number generation. These results show that some characteristics of observed finger, hand and mouth grip actions automatically prime number magnitude, with the strongest effect for finger grasping. The findings are discussed in terms of the functional and neural mechanisms shared between hand actions and number processing, but also between hand and mouth actions. The present study provides converging evidence that part of number semantics is grounded in sensory-motor mechanisms.

Keywords: random number generation, number magnitude, action observation, prehension

1. INTRODUCTION

Over the last decades, there has been an increasing number of studies testing grounded or embodied cognition theories. These theories postulate that cognition and knowledge are rooted in the sensorimotor systems (Barsalou, 2008; Barsalou, 2010), which are thus not only dedicated to action implementation but also contribute to conceptual and semantic processing through off-line sensorimotor simulations. For instance, as concerns concrete concepts, processing action words or tool names has been shown to recruit motor simulation processes (Buccino et al., 2005; Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005; Witt, Kemmerer, Linkenauger, & Culham, 2010). As concerns abstract concepts, an instance of embodiment of concept theories is the study of how numbers and other magnitudes are mentally represented, in which it is argued that numbers and action share common cognitive processes dedicated to magnitude processing (Chiou, Wu, Tzeng, Hung, & Chang, 2012; Lindemann, Abolafia, Girardi, & Bekkering, 2007; Wood & Fischer, 2008). A theory of magnitude (ATOM; Bueti & Walsh, 2009; Walsh, 2003) proposes that numerical quantities, time, space, and other magnitudes would be processed by a generalized magnitude system in the parietal cortices. Sensorimotor transformations, which also take place in the parietal cortex (Freund, 2001), would benefit from this system integrating different components of an input (e.g., size and location of an object) to implement the appropriate motor output (e.g., grip aperture amplitude or reaching trajectory). Thus, magnitude processing would be recruited to correctly compute actions with the right force, correct amplitude, and appropriate speed. Numbers would acquire part of their semantic meaning by being mapped on those magnitude representations arising through sensorimotor transformations. In support of this embodied view of number meaning, interactions between finger grasping actions and number processing have been reported, with numbers influencing the kinematics of grasping movements (Andres, Ostry, Nicol, & Paus, 2008; Lindemann et al., 2007; Moretto & di Pellegrino, 2008), or grasping action observation interfering with number processing (Badets, Bouquet, Ric, & Pesenti, 2012; Badets & Pesenti, 2011). Numerical processing and action implementation may thus share common cognitive processes and anatomical substrates within a generalized system dedicated to magnitude processing (here, numerosity and object size; Andres, Olivier, & Badets, 2008; Chiou, Chang, Tzeng, & Wu, 2009; Lindemann et al., 2007; Michaux, Pesenti, Badets, Di Luca, & Andres, 2010; Walsh, 2003). This system is thought to be located along the dorsal stream, a network of brain areas going from the early visual areas to the posterior parietal cortex, also involved in processing the location of objects in space and coordinating eyes and arms to guide saccades and reaching (Milner & Goodale, 1995; Walsh 2003). The links between numerical magnitude processing and grasp programming were first suggested by neuroimaging studies revealing neuro-anatomical overlaps between number processing and finger movement representation and control (Pesenti, Thioux, Seron, & De Volder, 2000). A fronto-parietal network including areas around the intraparietal sulcus (IPS) and a portion of the precentral gyrus was shown to be involved when participants were processing numerical magnitude or physical size (Fias, Lammertyn, Reynvoet, Dupont, & Orban, 2003; Pesenti et al., 2000; Pinel, Piazza, Le Bihan, & Dehaene, 2004; Santens, Roggeman, Fias, & Verguts, 2010), but also finger movements and representations (Andres, Michaux, & Pesenti, 2012; Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002; Tschentscher, Hauk, Fischer, & Pulvermüller, 2012), or the implementation of grasping hand movement (Castiello, 2005; Culham & Valyear, 2006; Ehrsson, Fagergren, & Forssberg, 2001). Studies have shown that the prefrontal cortex in monkeys is recruited when extracting the numerosity of items (Nieder, Freedman & Miller, 2002), and this activity is also considered to result from the representation of prospective goals (Genovesio, Tsujimoto & Wise, 2012; Stoianov, Genoveso & Pezzulo, 2016). The IPS and the premotor cortex are thus key areas for both magnitude representations and the implementation of goal directed grasping actions. Other studies have shown that semantic information about magnitude influences the planning and the kinematics of reach to grasp actions (e.g., Gentilucci & Gangitano, 1998; Glover & Dixon, 2002; Glover, Rosenbaum, Graham, & Dixon, 2004). These effects are interpreted as arising through affordance processes, which refer to the activation or selection of adequate action patterns from the properties of perceived objects (Gibson, 1979). For example, when participants are required to pick up objects, magnitude words written on these objects influence the kinematics of their grasp: the aperture of the grip during the early stage of the grasp is smaller when the word “short” is written on the objects compared to the word “long” (Gentilucci & Gangitano, 1998; Glover & Dixon, 2002). Similar effects have been found with words representing graspable objects that could either be small or large (Glover et al., 2004). The first study assessing this semantic–motor interaction using Arabic numbers showed that processing numbers interfered with finger grip opening and closing movements (Andres, Davare, Pesenti, Olivier, & Seron, 2004). In this study, participants were asked to judge whether a number was odd or even by opening or closing their finger grip; electromyographic recordings indicated that they initiated faster a grip closing in response to small numbers, while they initiated faster a grip opening in response to large numbers, and this in the absence of an object. Further studies demonstrated that the kinematics of object grasping were moderated by the magnitude of numbers presented on the objects (Andres et al., 2008; Chiou et al., 2012). Accordingly, precision grip actions on small object were facilitated by small number processing, while power grip actions on larger object were facilitated by large number processing (Lindemann et al., 2007; Moretto & di Pellegrino, 2008). These congruity effects arise automatically as participants were not explicitly asked to process the magnitude of these numbers. They also specifically affect the planning component since the kinematics were only influenced in the early stages of those movements (Andres et al., 2008; Glover & Dixon, 2002). Finally, these effects are also range-dependent, since the same number (e.g., *5*) induces either larger or smaller grip apertures when coupled with a smaller (e.g., *2*) or a larger (e.g., *8*) number respectively (Chiou et al., 2012).

Other studies have shown that the mere observation of grasping actions also influences number processing (Badets, et al., 2012; Badets & Pesenti, 2010, 2011), and have revealed both semantic–to–motor and motor–to–semantic number–grip interactions. For example, participants were asked to report the odd or the even digit of a pair as a function of the subsequent (i.e., semantic–to–motor) or the previous (i.e., motor–to–semantic) observation of a closing or an opening grasping action (Badets & Pesenti, 2010). In the semantic–to–motor condition, faster responses were observed for small numbers compared to large ones in case of grip closing observation, while faster responses for large numbers compared to small ones were observed in case of grip opening observation. In the motor–to–semantic condition, only grip closing observation influenced number processing. It is worth noting that non-biological fake hand actions had no influence on numerical processing, demonstrating that the effect does not emerge from mere low-level differences in perceiving opening/closing actions, but rather through object-directed action contexts (Badets & Pesenti, 2010). Likewise, only small/large graspable objects (e.g., *almond* or *coconut*) have been shown to interfere with number processing, while small and large ungraspable objects (e.g., *atom* or *cactus*) had no impact on number processing (Ranzini et al., 2011). In this latter study, the impact of action on number processing was therefore mediated by the physical size of the object affording either a large or a small grip. Finally, finger grip action observation also influences number production in a random number generation (RNG) task in which participants are required to randomly produce numbers (Badets et al., 2012). This RNG task has been shown to be moderated by the concomitant execution, observation or perception of body movements (e.g., head, eyes or full body; Grade, Lefèvre, & Pesenti, 2013; Hartmann, Grabherr, & Mast, 2011; Loetscher, Bockisch, Nicholls, & Brugger, 2008; Loetscher, Schwarz, & Schubiger, 2010). In the context of number-grip interactions, participants produced more small than large numbers after observing a finger grip closure than after observing a colour change, a grip opening action or fake hand closure and aperture (Badets et al., 2012). Only biological action observation moderated number processing, while non-biological action observation had no impact (Badets et al., 2012; Badets, Bidet-Ildei, & Pesenti, 2015). Together, all these studies strengthen the idea that the context of goal-directed prehension is determinant for the emergence of interactions between grasping actions and number processing.

So far, however, the interpretation of the number–grip interactions in terms of a shared magnitude code for number processing and object prehension remains indirect speculation, as it is not known whether any closing–opening action performed with a biological effector would elicit such an interaction with numerical magnitude or if only biological effector actions related to object prehension would work. Indeed, it has been shown that mouth opening movement control interacts with hand opening movement control (Gentilucci, Benuzzi, Gangitano, & Grimaldi, 2001), and that mouth and hand actions share some neural substrates (for a review, see Gentilucci, Dalla Volta, & Gianelli, 2008). Indeed, in order to correctly implement both grasping and ingesting movements, it is necessary to match the size of the objects or food piece with the amplitude of the hand or mouth aperture–closure. Moreover, it has been proposed that language is an embodied system where speech would have progressively developed from manual gestures rather than animal calls in the evolution of human communication (Corbalis, 2009; Gentilucci & Corbalis, 2006). Speech processes would have emerged partly within Broca’s area because this structure was already dedicated to the recognition of others' actions, a process that was determinant in interindividual communication (Rizzolatti & Arbib, 1998). Therefore, the cortical mechanisms involved in observing or implementing lip and hand movements might share processes and elicit similar effects on number processing.

In the present paper, we investigated how hand and mouth action observation and numerical processing may or may not interact by testing the possible influence of observing four different opening/closing actions on an RNG task. In the first action condition, precision finger grip was used to test its specificity on RNG compared to other closing/opening actions. In the second condition, full-hand opening and closing that did not directly refer to object prehension were used in order to investigate if the mere observation of biological closing and opening actions outside the context of object grasping would still influence RNG. In the third condition, opening and closing squeeze actions were used to investigate if this type of prehension could also moderate RNG. In the fourth action condition, opening and closing of the mouth were used to investigate if the observation of closing and opening actions realised with a biological effector other than the hand could also influence RNG. In line with previous results (e.g., Badets et al., 2012), we expected that observing finger grip actions should induce the strongest effect on number generation because it directly calls object prehension to mind. Then, if this interaction truly emerges from the (implicit) prehension context, observing hand grip action not directly related to prehension should not influence RNG as it would not depict an object-directed prehension action. Finally, observing squeeze and mouth actions might influence RNG, yet not as strongly as finger grip action, depending on whether these two actions call object interaction to mind for the participants.

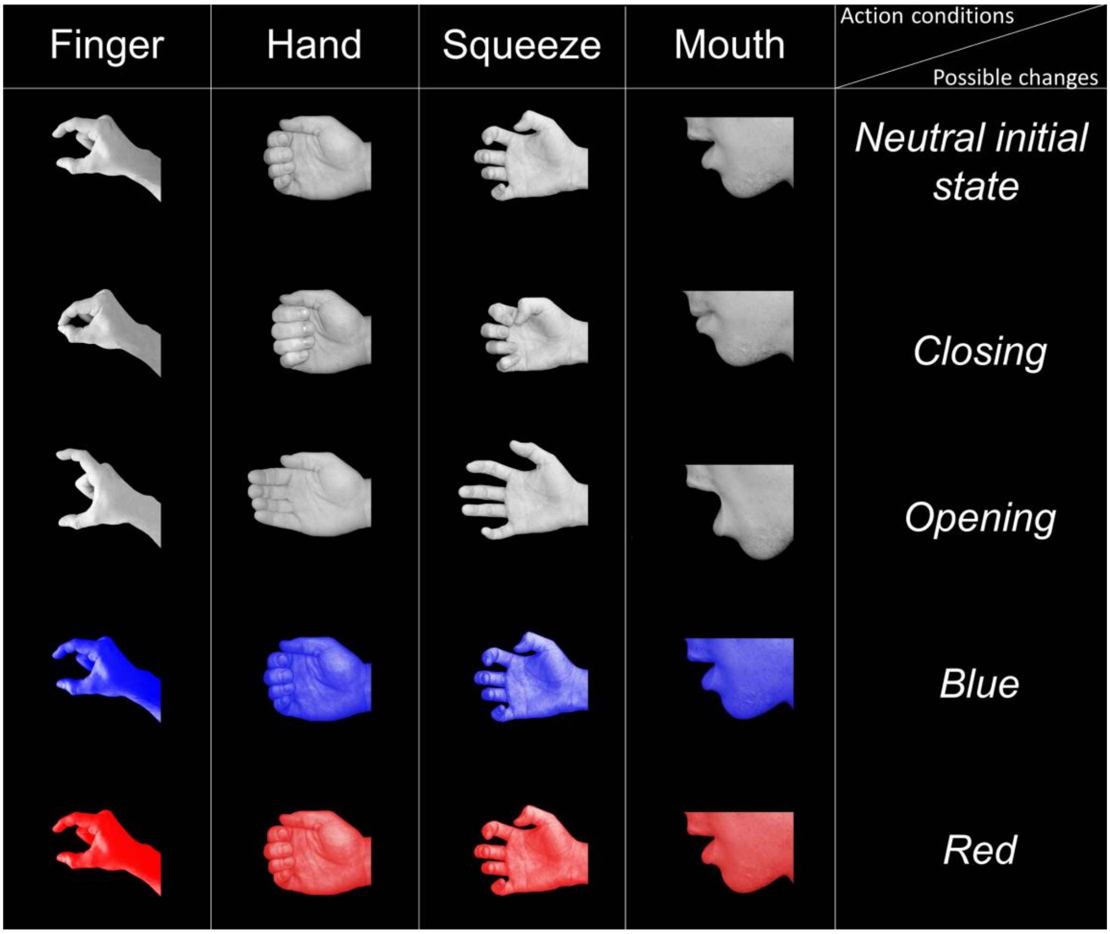
2. METHOD

2.1. Participants

Eighty undergraduate French-speaking students from the Université catholique de Louvain (54 female; 5 left-handed, 1 ambidextrous) took part in this study. They were all aged between 18 and 26 years (mean age = 19.8, *SD* = 1.5 years), had normal or corrected-to-normal vision, were unaware of the goal of the study prior to the experimentation, and had given their informed consent to participate. Twenty participants were randomly assigned to only one of the four action conditions. The experiment was non-invasive and was performed in accordance with the ethical standards established by the Declaration of Helsinki.

2.2. Apparatus and stimuli

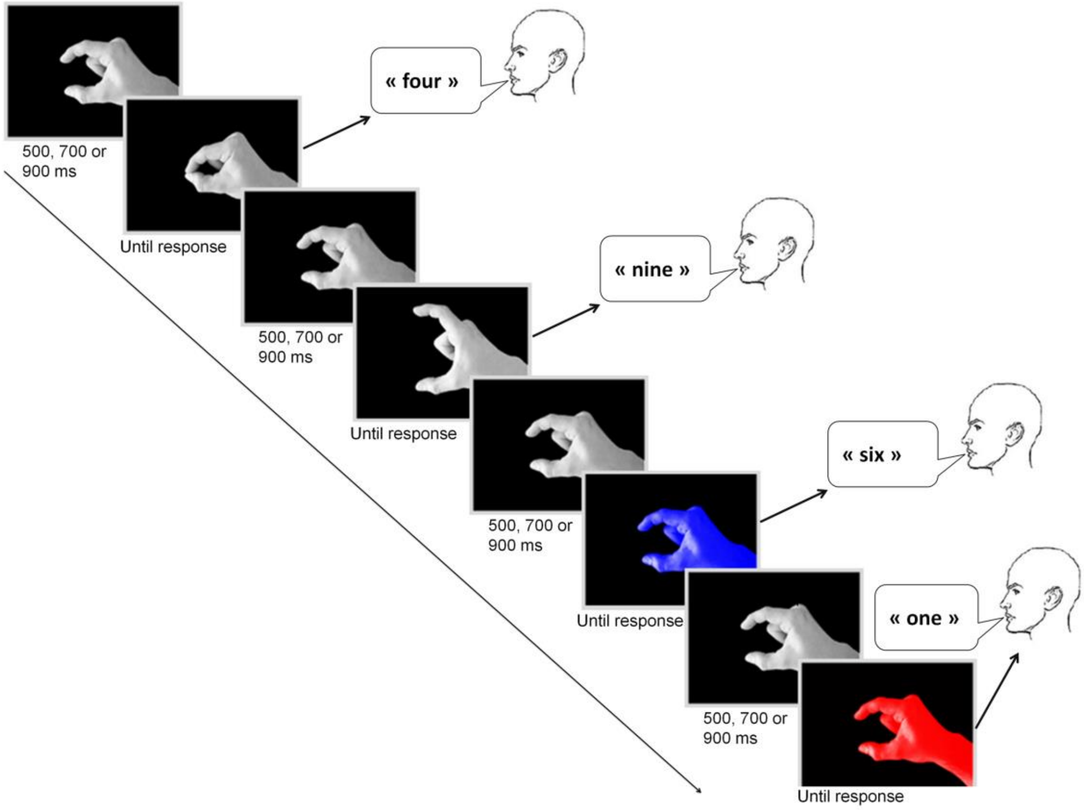
The experiment was conducted on a PC equipped with a 40 cm (diagonal) screen and a microphone. A customised E-prime programme (Schneider, Eshmann, & Zuccolotto, 2002) was used to control the experimental procedure. The stimuli consisted of pictures of a male right hand or mouth presented in shades of grey on a black background (see Fig. 1).



In the finger grip condition, the stimuli were the same as the ones used in Badets *et al.* (2012); they depicted precision grip opening and closing actions. In the hand grip condition, participants were presented with full-hand opening and closing actions that did not refer to object prehension as the thumb was static and only the four remaining fingers were moving. The squeeze grip condition showed full-hand opening and closing actions with the fingers being spread out from each other as would be done with a soft, squeezable ball. In the mouth action condition, the participants were presented with mouth opening and closing actions, photographed from a side profile view. For each of the four actions, a photograph showing a neutral intermediate amplitude was followed by one of four possible changes: either a change in the amplitude of the action inducing total closure or a wider aperture (action changes) or a change in colour (blue or red; colour changes) used as a control condition.

2.3. Procedure

The participants sat in front of the computer screen and the microphone. Depending on the action condition, each trial started with the presentation of the neutral posture of one of the action stimuli (see Fig. 2). After random durations of 500, 700 or 900 msec to prevent response anticipation, the neutral posture turned into one of the four possible changes (i.e., closing, opening, blue or red). The rapid succession of the two pictures led to the perception that the hand or mouth was actually moving in the action conditions (see animated GIF figures 1, 2, 3 and 4 in the Supplementary Material section). The beginning of the change was the trigger indicating to the participants that they had to respond; the final state of the change was displayed until response, which launched the next trial. The task was to speak aloud a number randomly selected between 1 and 10. The experimenter explicitly instructed the participants to avoid systematic ascending, descending or otherwise ordered sequences. The metaphor of a mental urn was suggested: the participants were asked to imagine a bag containing the ten numbers, to take one of them at each trial, put it back and start again for the next trial (for similar instructions, see Baddeley 1966; Badets et al., 2012, 2015; Grade et al., 2013; Loetsher & Brugger, 2007; Van der Linden, Beerten, & Pesenti, 1998). Additionally, they were told not to repeat the same number twice in a row. Within each of the four action conditions, the experiment consisted of two blocks of 216 trials; within a block, 54 trials of each of the four types of change were presented pseudo-randomly. To ensure the processing of the change, a parity rule was used. In the first block, participants were instructed to generate an odd number for closing or blue changes, and an even number for opening or red changes; this rule was reversed for the second block. The order of the two blocks was counterbalanced across participants. In order to familiarise participants with the task and make sure they understood the instructions, they performed a practice block (24 trials; 6 per change) before the experimental blocks. Emphasis was placed on respecting the parity rule rather than on the speed of responses, and no particular response time limit was imposed. For this reason, response latencies were not analyzed. The numbers produced were recorded on-line by the experimenter and were used to compute the dependent measures.



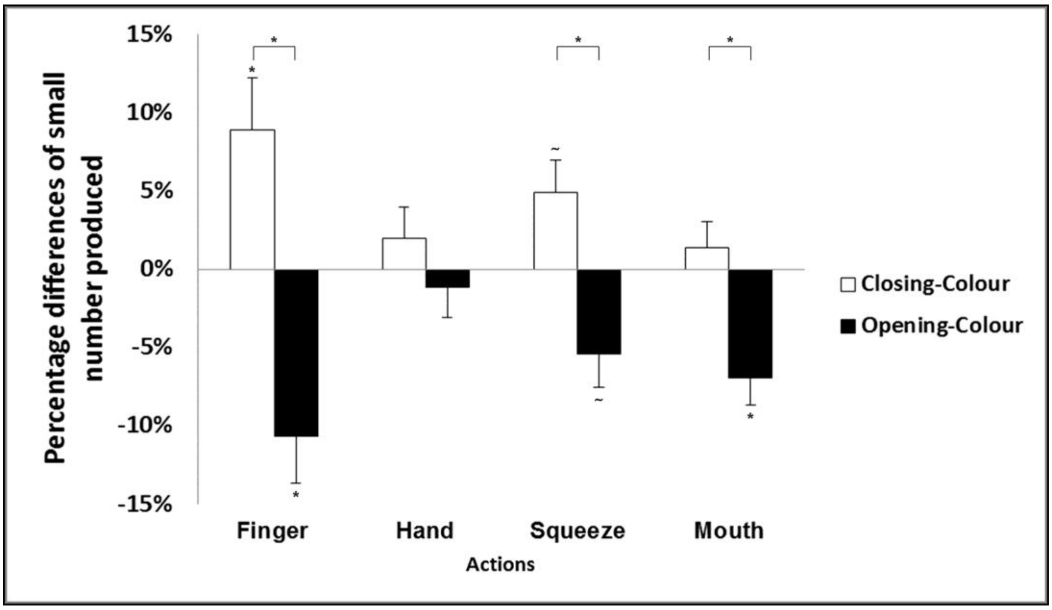
3. RESULTS

Unreliable trials due to coughs, noises or microphone failures (0.77% of the total data; *M* = 4.9*, SD* = 5.5), trials with breaches of the parity rule (3.04% of the total data; *M* = 13.7*, SD* = 9.4) and the non-repetition rule (1.7% of the total; *M* = 8.6*, SD* = 6.5) were not included in the analyses. The percentages of small (i.e., 1 to 5) and large (i.e., 6 to 10) numbers produced were computed separately for each participant and each type of change (closing, opening, blue and red); the analyses were carried out on the percentage of small numbers only since the percentage of large numbers is always the exact opposite within all valid productions (for similar analyses, see Badets et al., 2012, 2015; Grade et al., 2013; Loetscher et al., 2008). In order to get the best picture of the possible functional interactions between grip actions and numerical magnitude, 5 sets of analyses were carried out, each of them capturing a different aspect of the participants' RNG pattern.

To start, the baseline condition was analysed by testing whether the percentage of small numbers produced differed for the blue and red changes regardless of action conditions using *t*-test for paired samples. This was not the case (Blue: $M = 53.5$, $SD = 6.8$, Red: $M = 53.7$, $SD = 8.1$; $t(79) = 0.18$, $p > .05$). Then, we tested whether the percentage of small numbers produced for the blue or red changes differed within each action (i.e., finger, hand, squeeze *vs.* mouth) using analyses of variance (ANOVA). This was not the case either for the blue or for the red changes (both *ps* at least >.1). Therefore, the two colour changes were averaged for each participant to create a unique baseline colour change where no action was presented. The resulting values were also not influenced by action ($F(3, 76) = 0.62$, *ns*).

Then, to test whether the production of small numbers deviated significantly from chance level in the various change conditions, *t*-tests with 50 as the test value were performed on the percentage of small numbers for each change (i.e., opening, closing *vs.* colour). Where multiple comparisons were performed, a Bonferroni correction (BC) was applied (all reported *p*-values are two-tailed). The mean percentage of small numbers produced in the closing (mean % = 57.9, $SD = 8.7$; $t(79) = 8.05$, $p_{BC} < .001$), opening (mean % = 47.5, $SD = 8.9$; $t(79) = -2.4$, $p_{BC} = .05$), and colour (mean % = 53.6, $SD = 6.1$; $t(79) = 5.2$, $p_{BC} < .001$) changes were all significantly different from 50.

It is worth noting that comparing the percentage of small numbers produced to chance level does not take a possible natural small number bias (SNB) into account. Indeed, studies using RNG tasks frequently report a natural bias to produce more small than large numbers (e.g., Loetscher & Brugger, 2007). As participants produced more small numbers than chance level in the baseline pooled-colour change and to control any possible SNB for the closing and opening changes, we took this into account by subtracting the mean percentage of small numbers produced in the pooled-colour change from the percentage of small numbers produced in the closing and opening changes for each participant. The computed differences (i.e., [closing *minus* colour] and [opening *minus* colour]) were submitted to an ANOVA for repeated measures with the change (opening *vs.* closing) as a within-subject variable and the action (finger, hand, squeeze *vs.* mouth) as a between-subject variable. This analysis revealed a significant effect of the change ($F(1, 76) = 56.5$, $p < .001$), with the closing change (M = 4.2, SD = 10.7) having significantly more small numbers produced compared to the opening change (M = -6.06, SD = 10.4). There was no significant main effect of action ($F(3, 76) < 1$, ns). However, there was a significant interaction between the two factors ($F(3, 76) = 6.2$, $p < .001$; see Fig. 3). In order to decompose this interaction, each action condition was investigated separately with t-tests comparing the colour-corrected closing and opening changes to 0, and to each other. For the finger grip, the participants produced significantly more small numbers after the closing (M = 8.9, SD = 14.8; $t(19) = 2.69$, $p_{BC} < .05$) and significantly fewer after the opening (M = -10.6, SD = 13.3; $t(19) = -3.56$, $p_{BC} < .01$) corrected changes compared to 0; the two changes also differed from each other ($t(19) = 5.08$, $p_{BC} < .001$). For the hand grip, the differences did not differ from 0 in the closing (M = 1.9, SD = 9; $t(19) = 0.96$, $p_{BC} > .05$) and the opening (M = -1.1, SD = 8.6; $t(19) = -0.61$, $p_{BC} > .05$) changes; the two changes did not differ from each other ($t(19) = 1.5$, $p_{BC} > .05$). For the squeeze grip, the differences did not differ from 0 after the closing (M = 4.9, SD = 9.1; $t(19) = 2.4$, $p_{BC} > .07$) and the opening (M = -5.4, SD = 9.3; $t(19) = -2.5$, $p_{BC} > .05$) changes; nevertheless, the two changes differed from each other ($t(19) = 4.04$, $p_{BC} < .01$). Finally, for the mouth action, the differences did not differ from 0 for the closing change (M = 1.3, SD = 7.5; $t(19) = 0.79$, $p_{BC} > .05$) but did for the opening change (M = -6.9, SD = 7.8; $t(19) = -3.9$, $p_{BC} < .01$), and the two changes differed from each other ($t(19) = 3.8$, $p_{BC} < .01$; see Fig. 3).



Next, in order to investigate if the observed action would lead participants to produce a smaller or a larger number than the one produced at the previous trial, we calculated the proportion of numbers smaller than the one produced at the previous trial for each change and each participant separately. This analysis was restricted to numbers produced after a *5* or a *6* in order to balance the possibility of producing a smaller (i.e., 1, 2, 3 and 4) or a larger (i.e., 7, 8, 9 and 10) number. We then subtracted the values obtained for the colour change from those obtained in the closing and opening changes separately for each participant, and tested these mean differences against 0 and against each other using *t*-tests. For the finger grip, the participants significantly more often produced numbers smaller than the previous number produced after a closing change (mean difference = 0.13, $SD = 0.21$; $t(19) = 2.7$, $p_{BC} < .05$), and significantly less after an opening change (mean difference = -0.11, $SD = 0.17$; $t(19) = -2.8$, $p_{BC} < .05$). Moreover, the difference between those two differences was significant ($t(19) = 5.1$, $p_{BC} < .001$). For the hand grip, the participants did not produce more smaller numbers after either the closing (mean difference = 0.013, $SD = 0.18$; $t(19) = 0.32$, $p_{BC} > .05$) or the opening (mean difference = 0.006, $SD = 0.14$; $t(19) = 0.2$, $p_{BC} > .05$) changes; the difference between those differences was also not significant ($t(19) = 0.2$, $p_{BC} > .05$). For the squeeze grip, the participants did not produce more smaller numbers after either the closing (mean difference = 0.06, SD = 0.19; $t(19) = 1.3$, $p_{BC} > .05$) or the opening (mean difference = -0.08, SD = 0.19; $t(19) = -1.9$, $p_{BC} > .05$) changes. However, the gap between those differences was significant ($t(19) = 3.2$, $p_{BC} < .05$). For the mouth action, the participants did not produce more smaller numbers after either the closing (mean difference = 0.02, SD = 0.14; $t(19) = 0.74$, $p_{BC} > .05$) or the opening (mean difference = - 0.044, SD = 0.17; $t(19) = -1.1$, $p_{BC} > .05$) changes. The gap between those differences was also not significant ($t(19) = 1.5$, $p > .05$).[1]

Finally, the percentage of small numbers produced was investigated individually for each participant and for each change, using nonparametric binomial tests comparing the proportion of small/large numbers produced to chance level (i.e., 50%). Table 1 shows the number of participants who produced significantly more small than large numbers (or the reverse) as a function of changes and actions. Most participants produced significantly more small than large numbers after observing the closing change for the finger grip, and about half for the squeeze grip. Moreover, about half of the participants produced significantly more large than small numbers in the opening change for the finger grip. For all the other combinations of changes and actions, the vast majority of participants did not produce either more small nor more large numbers.

Insert Table 1 about here

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4. DISCUSSION

The aim of the present study was to assess the specificity of the number–grip interaction previously reported compared to other grasping actions by investigating if observing different types of biological closing and opening actions would impact an RNG task differently. Participants had to randomly produce numbers between 1 and 10 after perceiving a change (i.e., closing, opening or colour) on neutral finger, hand or mouth positions. We found that observing precision grip closing and opening had a significant impact on the random generation of a numerical response: closing finger grip observation led participants to produce more small numbers than large ones, while opening grip observation had the opposite effect. This replicates and extends previous findings that have been interpreted by the idea that these particular actions implicitly refer to object grasping, with the closure reflecting small object prehension and the aperture reflecting larger object prehension. Although squeeze grip observation had a weaker influence on RNG than finger grip actions, the observation of squeeze closing induced participants to produce significantly more small numbers that the observation of squeeze opening. In contrast to these effects of finger and squeeze grips, full hand grip observation clearly did not impact RNG. Compared to finger and squeeze grips, the shaping of the hand in this condition does not refer to object prehension, as the thumb remained static and no opposition between the fingers and the thumb was displayed, this being a key component of the formation of a prehension grip. The results thus show that merely observing finger or hand closing/opening actions is not sufficient to influence number production, as no influence was found in the hand grip and only a weaker influence in the squeeze grip. Together, these results raise the possibility that the more an action refers to prehension, the more its observation will moderate numerical processing. The present study thus goes one step further than merely replicating previous findings since it provides a firm demonstration that number–grip interactions arise only when an object-directed action context (here, prehension) is evoked by the stimuli (Badets, Andres, Di Luca, & Pesenti, 2007; Badets et al., 2012; Badets & Pesenti, 2010, 2011; Ranzini et al., 2011).

Interestingly, a large number bias in the opening change that had not been found in a previous action observation and RNG experiment (Badets et al., 2012) was observed here. It is worth noting that other previous studies (Andres et al., 2004; Badets & Pesenti, 2010; Lindemann et al., 2007) had already shown that hand opening actions can be associated with large number processing (e.g., large numbers facilitating grip opening or large object grasp). It is challenging to explain why an effect occurred on large numbers in the present study and not in Badets *et al.* (2012)'s study as the same stimuli were used in both experiments. In their discussion, Badets *et al.* (2012) argued that the absence of large number bias resulted from the fact that the opening finger grip action might have been perceived as a release rather than a grasp directed towards a large object. Therefore, since opening actions can refer both to the release of small and large objects, no influence was found on RNG. In the present study, we obtained a large number bias when participants observed finger grip opening, probably due to the fact that 45% of the participants (9/20) in the finger grip condition showed this open–large association, whereas a retrospective look at Badets *et al.* 's data showed that this was the case for only 25% of the participants (3/12). This suggests that participants in the present study might have interpreted the opening action as referring to large object grasping rather than to object releasing. Moreover, it is worth keeping in mind that the results come from two different groups of participants; hence, individual differences in motor imagery abilities across participants could explain the discrepancy (for a similar interpretation in action-number interactions, see Badets, Koch, & Toussaint, 2013). Indeed, the ability to perform action imagery varies among individuals and moderates action observation priming effects (Williams, Pearce, Loporto, Morris, & Holmes, 2012), this being in line with the fact that action observation and imagery activate similar cortical areas and might share common motor representations (Grèzes & Decety, 2001; Macuga & Frey, 2012). Future studies might assess more explicitly how the participants interpreted the stimuli, their imaginal capacities, and whether this affects the presence of the effect both for closure and aperture.

We have also shown that observing a mouth opening action led participants to produce significantly more large numbers than the colour change. This condition differed from the others, as it was the mouth instead of the hand/fingers that was the effector of the action. It has been shown that mouth and hand actions might share common processes (Gentilucci et al., 2001; Gentilucci et al., 2008) that could be related to processing object size. However, the action displayed might also refer to speech, breath or ingestion rather than to prehension. In the gestural-origin theory of speech (Corbalis, 2009; Gentilucci &

Corbalis, 2006), it is argued that speech evolved from hand gestures. The close connections between hand and mouth movements would have first been due to double grasp preparations in grasp-to-ingest movements, and then strengthened in the transfer from a manual gestural to a mouth articulation communication system (Gentilucci et al., 2001). Along with this, the sounds produced when pronouncing words would be linked to the meaning the words convey (the so-called “schematopoeia” theory; Paget, 1930). In the case of words coding magnitude, words representing largeness frequently contain open vowels, while words denoting smallness contain closed vowels (e.g., *large or huge* vs. *small or tiny*; Gentilucci & Corbalis, 2006). Therefore, pronouncing the word *large* causes the mouth to open wider compared to the word *small,* and the observation of a mouth getting wider might then have induced participants to randomly produce more large numbers. As suggested by a reviewer, mouth opening could also refer to breathing, more air being sent in the lungs while opening the mouth to breathe in deeply. Finally, mouth action could be related to food ingestion, as it is necessary to match the size of the piece of food with the amplitude of mouth aperture–closure, and his could be the reason why the closing mouth had no impact on the magnitude of the numbers produced, compared to the opening mouth. Indeed, when placing a piece of food in the mouth, it is the aperture of the mouth during the opening movement that needs to match the size of the piece of food, whereas the final state of the closing movement of the mouth is the same (i.e., no distance between the lips) whether a small or a large piece of food is ingested. How close the lips are is thus not informative about the actual size of the piece of food once inside the mouth. In contrast, in the case of the finger grip, the size of the object constrains the final aspect of the closing grip (i.e., varying distance between the fingers), as the object remains between the fingers and the closer the fingers, the smaller the object. The results of this mouth action condition are also in line with the idea of a generalized magnitude processing system (Bueti & Walsh, 2009; Walsh, 2003) that could recruit common size-related processes for planning and executing both hand and mouth actions. It is worth noting that the mouth stimuli used in the present study are not *a priori* more related to ingestion than to breath or speech, nor are the finger grip stimuli more related to grasping than to aperture/closure. As a matter of fact, the instructions given to the participants never mention these actions, but only use the terms aperture/closure that describe what the participants would see. Relating the closing/opening finger grip to prehension and mouth to ingestion is thus our own *post-hoc* interpretation. As concerns finger grip, this interpretation is supported by our previous studies showing that nonbiological opening/closing grip stimuli does not interfere with number processing (Badets & Pesenti, 2010), nor do biological finger grips when no prehension intention is present in the task (Badets et al., 2007). For the mouth stimuli, no such previous support exists, but the link with ingestion seems to us plausible given the effect on the opening action only.

Finally, concerning the colour changes, the results indicated that participants produced slightly more small numbers than chance level when taking the overall mean. Moreover, when investigating each participant's number generation profile individually, a fifth of the sample produced significantly more small numbers than chance level in the colour change, regardless of action condition. This can be attributed to what has been termed the SNB, an effect that is frequently observed in RNG tasks (Loetscher & Brugger, 2007). This bias is thought to be due to the fact that small numbers are more frequently used compared to large ones or to the fact that the mental number space would be compressed and could elicit pseudoneglect in RNG tasks favouring small numbers. Our results also show that the percentage of small numbers produced after a colour change was not moderated by the actions, and did thus not differ across finger, hand or mouth neutral postures changing colours. This excludes an interpretation of the stronger effect observed with the finger grip as being merely due to specific configurational aspects of finger gestures related to some conventional communicative functions[2], because in this latter case the neutral finger grip should already lead to producing more small numbers than the other actions.

Overall, this study shows that the mere observation of finger, hand and mouth actions influences an RNG task. It seems, though, that the more an action refers to object prehension, the more its observation influences numerical processing: precision finger grip and hand squeezing actions do refer to object prehension whereas full-hand closure/aperture does not. This interpretation brings an additional piece of evidence that number–motor interactions arise only with relevant object-directed actions. These interactions might take place because numerical magnitude and object-directed grasping actions are both represented within a very close if not overlapping fronto-parietal network along the dorsal stream (Badets et al., 2012; Badets & Pesenti, 2010; Castiello, 2005; Pesenti et al., 2000; Simon et al., 2002; Stoianov et al., 2016). Moreover, they also fit within the ATOM proposal (Bueti & Walsh, 2009; Walsh, 2003) that postulates a core system for the processing of various magnitudes. This could imply that both perceiving the size of an object and implementing the appropriate grip aperture in order to correctly interact with it would recruit this general magnitude-processing system. Numerical representations then could be mapped and be rooted in this magnitude system that arises because of the need to having a system able to process magnitudes for both perception and action. These theoretical assumptions are in line with the idea that the meaning of abstract concepts (here, number meaning) is embodied in sensory-motor processes (Barsalou, 2008). Therefore, magnitude processes taking place in the dorsal stream responsible for object-directed actions might mediate the number-grip interactions that have been observed in the present study and in several previous ones.

In conclusion, our findings show that the production of numbers can be moderated by the concomitant observation of object-directed prehension actions, even if no objects are present in the visual scene. Moreover, we have shown that the mere observation of closing and opening body parts not related to an object-directed prehension context is insufficient to influence number production. We have also shown that, although this link is weaker than with finger or hand grasping actions, mouth actions and numerical magnitude are related, possibly through the adjustment of mouth aperture amplitude to food size during ingestion. These results suggest that the perceptual-motor system contributes to the representation of magnitude and, more specifically, to the representation of numerical magnitudes. They support the view that the cognitive processes representing the meaning of numbers may partly arise from sensorimotor transformations involved in the implementation of goal-directed actions.

Footnotes:

[1] This fourth analysis was limited to the investigation of the proportion of ascending or descending responses compared to the previous one. Two elements were not included in this analysis: it did not take into account the magnitude of the difference between two numbers consecutively produced (i.e., numerical distance), and it was not limited to responses occurring after the production of *5* or *6*. Two additional analyses were conducted in order to take into account (1) the numerical distance and (2) the overall descending/ascending expected probability based on the actual productions of each participant, which was then compared to the actual proportion of observed increase/decrease. These two sets of analyses confirmed the results of the current analyses: they can be found in the Supplementary Material section of the present article.

[2] As suggested by an anonymous reviewer on a previous version of this article, it is not uncommon to use a conventional gesture involving the index finger and the thumb to refer to small magnitudes or distances (e.g., *"The bullet passed this close to my head"*).

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Table 1. Number of participants producing significantly more small than large numbers (A) or the reverse (B) as a function of changes and actions (out of 20 participants per action).

	(A) More Small			(B) More Large		
	Closing	Opening	Colour	Closing	Opening	Colour
Finger	14	0	4	2	9	1
Hand	5	3	3	1	0	0
Squeeze	10	2	4	0	3	1
Mouth	5	1	4	0	3	0

Figure Captions

Figure 1. Stimuli used in the four action conditions (finger; hand; squeeze and mouth from left to right columns). The first row shows the stimuli of the neutral initial positions; the second row shows the stimuli in closing position; the third row shows the stimuli in opening position. The two last rows show the *blue* and *red* stimuli, which were the same as the neutral stimuli but displayed in colour.

Figure 2. Temporal sequence of possible trials in the finger grip condition (which was the same for the other action conditions). For each trial, the stimuli in the neutral position was displayed and changed into closing, opening, *blue* or *red* stimuli.

Figure 3. Differences in the percentage of small numbers (1 to 5) produced in the two position changes (closing or opening) compared to the colour change (baseline) in the four action conditions. The white bars represent the differences between the closing and colour changes while the black bars represent the differences between the opening and colour changes. ***** = significant difference when compared to 0; **~** = significant difference from zero without Bonferroni correction; *** over bracket** = significant difference between the two corrected movement changes; error bars represent 1 *S.E.M.*